EVALUATING THE EFFICACY OF PREDATOR MANAGEMENT CONCURRENT WITH CHANGES IN PREY COMMUNITIES

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Robin Lynn DeBruyne

August 2014

EVALUATING THE EFFICACY OF PREDATOR MANAGEMENT CONCURRENT WITH CHANGES IN PREY COMMUNITIES

Robin Lynn DeBruyne, Ph. D.

Cornell University 2014

Double-crested cormorants (*Phalacrocorax auritus*; hereafter cormorants) are piscivorous waterbirds considered top predators in aquatic systems. In order to accurately evaluate effects of cormorants on prey fish, several pieces of information which overlap in space and time are needed: (1) cormorant abundance and consumption in the study system; (2) cormorant diet composition; and (3) accurate information on prey abundance in the system. This research expands the knowledge of bird-fish interactions and predator-prey, dynamics and evaluates the effects of predator removal and changing prey communities. I examine patterns in cormorant consumption and how consumption was influenced by changing prey communities in two large lakes, Lake Champlain and Oneida Lake, New York. I also examine percid population dynamics in response to the removal of cormorants from Oneida Lake. Cormorants were found to significantly affect walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) subadult survival in Oneida Lake and were subsequently managed on the lake. This research evaluates the efficacy of cormorant management on Oneida Lake by utilizing the long-term data set available for cormorants and the fish community.

I document spatial and temporal variation in cormorant diets in Lake Champlain and Oneida Lake associated with changes in prey fish communities, specifically alewife (*Alosa psuedoharengus*) establishment in Lake Champlain and gizzard shad (*Dorosoma cepedianum*)

resurgence in Oneida Lake. Also, cormorants were found to select for and switch to emerald shiner (*Notropis atherinoides*) and gizzard shad when present in Oneida Lake. Gizzard shad were found to buffer yellow perch from cormorant consumption. Cormorant management resulted in decreased percid subadult; however, it should be noted that the prey fish community and cormorant diets shifted at this time as well. Only the walleye adult population reached the expected abundance. Yellow perch failed to reach predicted adult abundance, likely due to low age-1 abundances, possibly a result of walleye, largemouth bass, and smallmouth bass predation on age-0 and age-1 yellow perch. Cormorant management implemented to protect sportfishes should include fish abundance and cormorant diet monitoring to influence management actions and adapt them if impacts to sportfish change.

BIOGRAPHICAL SKETCH

Robin was born on February 26, 1982 in Portsmouth, Virginia to Lee and Shari (Danforth) DeBruyne. She grew up in Erie, Michigan where she spent many days on western Lake Erie fishing for walleye and yellow perch with her dad and grandpa, and enjoying all that Lake Erie has to offer. Robin graduated valedictorian from Mason High School in 2000 and attended Central Michigan University (CMU) that fall, majoring in Biology and minoring in Chemistry. While at CMU she worked as a fisheries technician in northern Lake Michigan at the CMU Biological Station on Beaver Island, at the Michigan Water Resource Center, and in the laboratory of Dr. A. Scott McNaught assisting with larval fish research in Lake Michigan. Robin graduated with honors with a BS from CMU in May 2004. She began her Master's Degree research at CMU right away under Dr. Tracy Galarowicz examining changes in growth and relative abundance of lake whitefish in Lake Michigan. Robin graduated with her MS in Biology, with a Conservation Concentration, from CMU in December 2006. She enrolled in the Ph.D. program at Cornell University in the Natural Resources department in May 2007 under the guidance of Dr. Lars Rudstam. Her doctoral research evaluated the walleye and yellow perch population responses to the removal of cormorants on Oneida Lake, New York. She married Justin A. Chiotti in 2008, and had two children, Braelynn (in 2009) and Brennan (in 2011) while completing her dissertation. She resides with her family in Hartland, Michigan and is employed as a contractor for the U.S. Geological Survey Great Lakes Science Center in Ann Arbor, Michigan.

For my family that provided all their love and support;

for Lee Alan;

and especially for Justin and our beautiful children that inspire me every day.

ACKNOWLEDGMENTS

This research would not have been possible without the effort of many individuals and I would like to start by acknowledging and thanking my committee members for all of the time and effort they contributed to my graduate research and experience at Cornell University. Lars Rudstam and Randy Jackson served as my daily sound boards for ideas and guidance. I am sure it was not always been easy, and I indebted to them for their efforts. Pat Sullivan was my statistical and biometry mentor. His patience is unparalleled and I am benefactor of his teaching and guidance. Mike Richmond brought me into the bird ecology world, and kept me thinking of big-picture implications. Travis DeVault provided additional research opportunities and guidance throughout, always stressing the implications of cormorant management to my research. I feel my committee was diverse, but these differing expertises were extremely beneficial in keeping me objective and thoughtful when working on a controversial topic. I cannot express the level of gratitude and appreciation I have for them working with me these past seven years. I am truly lucky to have worked with each. I would also like to acknowledge and thank my other coauthors for their efforts on two of my chapters which have already been published: Adam Duerr, David Capen, Fred Pogmore, Jeremy Coleman, and Tony VanDeValk.

The Lake Champlain and Oneida Lake cormorant diet work would not have been possible without the efforts of the USDA Animal and Plant Health Inspection Services, Wildlife Services staff of Vermont and New York. Thank you for coordinating your cormorant collections to make my study possible. I would also like to thank my two undergraduate interns, Jackie Chen and Katie Wu, for processing the cormorant diets while having fun!

The long-term fish and cormorant monitoring data on Oneida Lake would not have been possible without the efforts of many, many researchers, technicians, staff, graduate students, and interns over the past 50+ years. For my time and research at the Cornell Biological Field Station, I would like to thank John Forney, Tom Brooking, JoAnne Getchonis, Kristen Holeck, Scott Kruger, Jonathan Swan, Brian Young, and Bill Thelan for their advice, assistance, and good humor. I would like to especially thank Willie Fetzer, Tony VanDeValk, and Jeremy Coleman for many, many discussions about Oneida Lake fisheries and cormorants.

The graduate students in the Department of Natural Resources also provided excellent mental support and I hope I was able to return the favor. Thank you to Dan Bogan, Laura Eierman, Kim Falbo, Paul Simonin, and Heather Vandenberg Treizenburg. I thank the department for the support of the Director of Graduate Studies, Cliff Kraft and Shorna Allred, and the administrative staff, Ellen Harris, Erin Kelly, Christie Sayre, and Melinda vonGordon.

Finally, I would like to thank my family for all of their love and support for the past 14 years when I have been a college student. It seemed like it would never end, but it has. Thank you so much mom, Dave, Grandma Danforth, and Amanda. The biggest thank you and the most appreciation must go to Justin who, along with Milo, followed me to New York and supported me as I continued to push to the end. Thank you for everything.

This work was funded by a grant from USDA Animal and Plant Health Inspection Services, Wildlife Services, continued support from New York Department of Environmental Conservation, New York Federal Aid Project F-56-R to the Cornell Warmwater Fisheries Unit, the Cornell University Department of Natural Resources as a teaching assistantship, and a Kieckhefer Adirondack Fellowship.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

PREFACE

"Likewise, although man himself is the greatest predator the world has ever known, he tends to condemn all other predators without bothering to find out if they are really detrimental to his interests or not."

~ E. Odum, *Fundamentals of Ecology*, 2nd Edition

Aquatic predators can significantly impact their prey and the ecosystem (Brooks and Dodson 1965; Carpenter et al. 1985; Mills et al. 1987). Direct impacts to their prey can come through predation mortality, altered behavior or habitat choice, or growth changes (Werner et al. 1983; Sih 1987; Lima and Dill 1990; Tonn et al. 1992). Indirect impacts to their prey and the ecosystem arise from responses in food web interactions (Colby et al. 1987; Mittelbach and Chesson 1987; Polis 1991; Polis and Holt 1992; Rose et al. 1999). Double-crested cormorants (*Phalacrocorax auritus*; hereafter cormorants) are piscivorous waterbirds considered top predators in aquatic systems. Even though studies indicate no significant direct competition between fisherman and cormorants for prey species (VanDeValk et al. 2002; Carpentier et al. 2003; Barks et al. 2010; Ridgeway et al. 2012), much effort has been expended attempting to evaluate what effect, if any, cormorants have on recreational and commercial fish species. In order to accurately evaluate effects of cormorants on prey fish, several pieces of information which overlap in space and time are needed: (1) cormorant abundance and consumption in the study system; (2) cormorant diet composition; and (3) accurate information on prey abundance in the system. Each of these three basic pieces of information may need to be assessed multiple times or at specific levels of detail (e.g., temporal changes in cormorant abundance or prey availability; cormorant consumption and the availability of abundance estimates specific to the consumed size or age of prey population). This level of detailed monitoring for predators and prey is rare, especially for predators (e.g., cormorants) which consume multiple prey species. In most systems where cormorant-fish interactions have been examined (with varying degrees of complete

information described above), most have concluded that cormorant effects on fish populations are not significant, meaning their effects are not negatively affecting a sport or commercial fishery in a measurable manner (Cowx 2003; Wires et al. 2001; Wires 2014).

This research expands the knowledge of bird-fish interactions and predator-prey, dynamics and evaluates the effects of predator removal and changing prey communities on what is considered a generalist predator. Cormorants affect their prey through direct consumption, but possibly more importantly, they indirectly affect other predators (including recreational and commercial fisheries) ability to use the prey species. I examine patterns in cormorant consumption and how consumption was influenced by changing prey communities in two large lakes, Lake Champlain and Oneida Lake, New York. I also examine percid population dynamics in response to the removal of cormorants from Oneida Lake. Cormorants were found to significantly affect walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) subadult survival in Oneida Lake (Rudstam et al. 2004) and were subsequently managed on the lake. This was a rare opportunity to conduct and analyze a whole-lake experiment and measure in detail the responses of the fish community (Walters and Holling 1990). This research evaluates the efficacy of cormorant management on Oneida Lake by utilizing the long-term data set available for cormorants and the fish community. Previously confounding ecosystem factors (e.g., zebra mussels [*Dreissena polymorpha*]) have been evaluated (Rudstam et al. *in press*) and these effects on the percid populations can be parsed from effects due to cormorants.

Study Sites

Lake Champlain is located between the states of New York and Vermont, USA and Quebec, Canada and drains into the St. Lawrence River. Lake Champlain is a long (193 km) and narrow (20 km at widest point) lake that supports coldwater fisheries, such as lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*) and warmwater fisheries, such as yellow perch, smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*M. salmoides*)

(Marsden and Langdon 2012). Alewife (*Alosa pseudoharengus*) were first observed in Lake Champlain in 2003 and by 2007 had spread throughout the lake and are reproducing naturally (Marsden and Hauser 2009). Cormorants on Lake Champlain have been managed by federal and state agencies to minimize the destruction of vegetation and concomitant effects on co-nesting species. In 1999, an egg-oiling program was initiated on the Grand Isle, VT to reduce reproductive success and control population levels of nesting cormorants. Management later included a culling program to more rapidly reduce cormorant numbers as a means of restoring native vegetation to the colony island. In the past decade, anglers have also expressed concerns about cormorant foraging on local sportfish populations, particularly yellow perch.

Oneida Lake is a shallow, moderately productive lake with a surface area of 207 km^2 (Mills et al. 1978). Oneida Lake is the largest lake contained entirely within the State of New York and has a valuable recreational fishery for walleye, yellow perch, smallmouth bass and largemouth bass (Connelly and Brown 1991; VanDeValk et al., in press). Zebra mussels were discovered in the lake in 1991 and quagga mussels (*D. bugensis*) arrived around 2005 (Mills et al., in press). The colonization of the lake by zebra mussels was followed by increased water clarity (Idrisi et al. 2001), increased in macrophyte coverage (Zhu et al. 2006), as well as changes in the benthic community (Mayer et al. 2002, in press). Double-crested cormorants first nested on Oneida Lake in 1984 (Claypoole 1988). Nest counts increased steadily from 1984, peaking at 365 nests in 2000 (Coleman 2009). Migrating cormorants also stop-over on Oneida Lake, typically arriving in August and remaining on the lake through October. Total daily abundances also increased over time and were found to exceed 2000 individuals in 1996 and 1997 (Rudstam et al. 2004; Coleman 2009). Cormorant management was initiated in 1991 with a series of progressively more restrictive management actions enacted through 2009. Cormorant management escalated from restricting nesting locations to non-lethal harassment through the entire breeding and migration seasons, limited lethal take, nest destruction, and egg oiling of all nests on the lake.

Summary of Main Findings

Importance of spatial and temporal variation in predator diets

Spatial variability in cormorant diets was known to exist over large geographic scales (Newman et al. 1997; Wires et al. 2001), however the level of variability within a single lake, or from birds from a single colony, was not as well documented. In Chapter 1, I examined cormorant diets from Lake Champlain and documented diets were significantly different based on collection or colony location within the lake. These results can be used to target cormorant management to specific areas of Lake Champlain where species of interest (e.g, yellow perch) are being consumed in large numbers. It should be noted that no fish abundance information was available to compare with diet information for Lake Champlain, so the actual impact of cormorant consumption on the fish population parameters (e.g., mortality) is not known.

Cormorant diets are also known to vary temporally through the breeding season or between a few years; however few locations have extended diets information as part of long-term monitoring (but see Johnson et al. 2002, 2010). In Chapters 1 and 2, I document temporal variation in cormorant diets in Lake Champlain and Oneida Lake associated with changes in prey fish communities. Alewife establishment in Lake Champlain and gizzard shad (*Dorosoma cepedianum*) resurgence in Oneida Lake changed cormorant diets by both of these non-native species becoming a dominant diet item during specific seasons. Also, because Oneida Lake has a long-term fish community monitoring program, cormorant prey selectivity and prey switching was evaluated. Cormorants were found to select for and switch to emerald shiner (*Notropis atherinoides*) and gizzard shad when present in Oneida Lake. Gizzard shad were found to buffer yellow perch from cormorant consumption. Other systems which have soft-bodied fish present may also have similar sportfish buffering occurring, however caution should be used when extrapolating diet information to other systems. Given the cormorant diet changes observed in these two systems, evaluating potential or realized cormorant

impacts to the fish community based on local diet information is best.

Efficacy of predator management to reduce percid subadult mortality

Based on conclusions in Rudstam et al. (2004), cormorant management on Oneida Lake was anticipated to reduce subadult mortality of walleye and yellow perch. Consequently, reduced cormorants abundance on the lake was expected to reduce predation on the fish community, allowing for more age-1 walleye and yellow perch to recruit into the fishery. Based on Chapters 2 and 3, cormorant management, which began in 1998 and intensified in 2004, reduced subadult percid mortality. The age-1 to adult percid recruitment returned to the pre-1989 relationship and cormorants were found to have consumed few percids since 2001 (Chapter 3). However, it should be noted that the prey community shifted at this time and cormorants were not consuming percids in the fall; instead they were consuming gizzard shad in large amounts (Chapter 2). The reduction in cormorant abundance undoubtedly reduced the percid subadult mortality induced by cormorant predation during the mid-1990s; however the shift in consumption to non-percids likely resulted in a stronger manipulation of the system and further reduced percid subadult mortality.

Importance of alternative predators to prey population dynamics

Concurrent with decreased subadult mortality associated with reduced cormorant management, the adult percid populations were expected to increase as more subadults recruit to the fishery (Rudstam et al. 2004). Percid subadult mortality was found to decrease and adult percid populations increased from their lowest levels during the 1990s; however only the walleye adult population reached the expected abundance (Chapter 3). Using simulation modelling, increased age-1 to adult survival associated with cormorant management and increased adult survival associated with changed harvest regulations accounted for 29% and 44% of the observed increase in adult walleye abundance, respectively (Chapter 3). Yellow

perch failed to reach predicted adult abundance, likely due to low age-1 abundances, possibly a result of walleye, largemouth bass, and smallmouth bass predation on age-0 and age-1 yellow perch (Fetzer 2013).

Recommendations for Fishery Management

Using well-studied systems to evaluate predator-prey interactions and the efficacy of predator management is advantageous because data is collected in the detail needed to accurately assess the impacts of management. Even so, applying the results of well-studied systems, such as Oneida Lake, to other systems should be done with caution. Studies in Oneida Lake and eastern Lake Ontario (another well-studied system in the Great Lakes) concluded cormorants were responsible for declines in sportfish abundance by causing increased subadult mortality (Burnett et al. 2002; Lantry et al. 2002; Rudstam et al. 2004). More recently, both systems have seen dramatic shifts in cormorant dies which change the impact projections of cormorants on the sportfish of interest (Johnson et al. 2010; Chapter 2). While these systems are models for what cormorant impacts can be, they are also models for how rapidly impacts can change. Cormorant management implemented to protect sportfishes should include fish abundance and cormorant diet monitoring to influence management actions and adapt them if impacts to sportfish change.

Also, monitoring of other predators diets (and angler harvest if applicable) would identify and quantify all sources of mortality for the species of interest. Cormorant impacts are often assessed through modelling exercises (Seefelt and Gillingham 2008; Meihls et al. 2009; Schultz et al. 2013; Rutherford and Rose *in press*), which rely on accurate inputs of consumption for all predators to provide reliable and contemporary assessments of the modeled system. Understanding prey selectivity, and how this selectivity affects predator diets, would further improve model performance, especially when the selected prey species is abundant (Chapter 2). This sensitivity to the diet input information can result in inaccurate predictions if not updated, making the need to monitor and understand any variations in

consumption habits critical.

Finally, I cannot overemphasize the value of long-term monitoring data. Fish populations exist in ecosystems with more than only their predators and prey. Aquatic ecosystems are complex with many interactions which resonate through the food web; therefore removing top predators may affect the system in unanticipated ways (Yodzis 2000, 2001). The long-term monitoring data available for Oneida Lake allowed for prey-fish survival estimates to be calculated before and after cormorants were present, adult percid population trends to be evaluated and previously confounding factors (Rudstam et al. 2004) to be evaluated separately. Ultimately, managers must define the goals and objectives of any predator management program and should monitor the appropriate predator and prey parameters accordingly (e.g., cormorant diets, prey abundance and mortality). If detailed monitoring is not occurring, there is no way to confidently assess whether management actions are being effective or aiding the species of interest (Chapter 3). Accurately monitoring predator and prey population characteristics for measurable and numerical responses in association with management actions is the best way to evaluate if the time, effort, and financial investment in predator management was successful; without careful monitoring, any anecdotal changes in predator or prey population conditions can at best be categorized as correlated with management, not a result of management.

Literature Cited

Barks, P. M., J. L. Doucette, and C. M. Somers. 2010. Lack of angling-sized yellow perch in a Canadian boreal lake: potential influences of growth rate, diet, and predation by double-crested cormorants. Transactions of the American Fisheries Society 139: 1029-1040.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150(3692): 28-35.

Burnett, J. A. D., N. H. Ringler, B. F. Lantry, and J. H. Johnson. 2002. Double-crested cormorant predation on yellow perch in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 202–211.

Carpentier, A., J. M. Paillisson, and L. Marion. 2003. Assessing the interaction between cormorants and fisheries: the importance of fish community change. Pages 187-195 in I. G. Cowx, editor. Interactions between fish and birds: implications for management. Fishing News Books, Blackwell Science, Oxford.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634-639.

Claypoole, K. 1988. First nesting of the double-crested cormorant at Oneida Lake, New York. Kingbird 38: 235–236.

Colby, P. J., P. A. Ryan, D. H. Schupp, and S. L. Serns. 1987. Interactions in north-temperate lake fish communities. Canadian Journal of Fisheries and Aquatic Sciences 44 (Suppl. 2): 104-128.

Coleman, J. T. H. 2009. Diving behavior, predator-prey dynamics, and management efficacy of double-crested cormorants in New York State. Doctoral dissertation. Cornell University, Ithaca, New York.

Connelly, N. A., and T. L. Brown. 1991. Net economic value of the freshwater recreational fisheries of New York. Transactions of the American Fisheries Society 120: 770–775.

Cowx, I. G., editor. 2003. Interactions between fish and birds: implications for management. Fishing News Books, Blackwell Science, Oxford.

Fetzer, W. W. 2013. Disentangling the effects of multiple ecosystem changes on fish population and community dynamics. Doctoral dissertation. Cornell University, Ithaca, New York.

Idrisi, N., E. L. Mills, L. G. Rudstam, and D. J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New

York. Canadian Journal of Fisheries and Aquatic Sciences 58: 1430–1441.

Johnson, J. H., R. M. Ross, and R. D. McCullough. 2002. Little Galloo Island, Lake Ontario: a review of nine years of double-crested cormorant diet and fish consumption information. Journal of Great Lakes Research 28: 182-192.

Johnson, J. H., R. M. Ross, R. D. McCullough, and A. Mathers. 2010. Diet shift of double-crested cormorants in eastern Lake Ontario associated with the expansion of the invasive round goby. Journal of Great Lakes Research 36: 242-247.

Lantry, B. F., T. H. Eckert, C. P. Schneider, and J. R. Chrisman. 2002. The relationship between the abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 193–201.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Marsden, J. E., and M. Hauser. 2009. Exotic species in Lake Champlain. Journal of Great Lakes Research 35: 250-265.

Marsden, J. E., and R. W. Langdon. 2012. The history and future of Lake Champlain's fishes and fisheries. Journal of Great Lakes Research 38: 19-34.

Mayer, C. M., R. A. Keats, L. G. Rudstam, and E. L. Mills. 2002. Scale-dependent effects of zebra mussels on benthic invertebrates in a large eutrophic lake. Journal of the North American Benthological Society 21: 616-633.

Mayer, C. M., B. Zhu, and R. Cecala. The zebra mussel invasion of Oneida Lake: benthification of a eutrophic lake. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Miehls, A. L. J., D. M. Mason, K. A. Frank, A. E. Krause, S. D. Peacor, and W. W. Taylor. 2009. Invasive species impacts on ecosystem structure and function: A comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. Ecological

Modelling 220: 3194-3209.

Mills, E. L., J. L. Forney, M. D. Clady, and W. R. Schaffner. 1978. Oneida Lake. Pages 367-451 in J. A. Bloomfield, editor. Lakes of New York State. Volume II. Academic Press, New York.

Mills, E. L., J. L. Forney, and K. J. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. Pages 118-131 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Mills, E. L., J. L. Forney, and K. T. Holeck. Oneida Lake: a century of biotic introductions and ecosystem change. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Mittelbach, G. G., and P. L. Chesson. 1987. Predation risk: indirect effects on fish populations." Pages 315-332 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Neuman, J., D. L. Pearl, P. J. Ewins, R. Black, D. V. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54: 1569–1584.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138: 123-155.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology & Evolution 7: 151-154.

Ridgway, M. S., W. I. Dunlop, N. P. Lester, and T. A. Middel. 2012. Relative demand by double-crested cormorants and anglers for fish production from lakes on Manitoulin

Island, Lake Huron. Journal of Great Lakes Research 38: 514-523.

Rose, K.A., E. S. Rutherford, D. S. McDermot, J. L. Forney, and E. L. Mills. 1999. Individual-based model of yellow perch and walleye populations in Oneida Lake. Ecological Monographs 69: 127-154.

Rudstam, L. G., A. J. VanDeValk, C. M. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14: 149–163.

Rudstam, L. G., E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Rutherford, E. S., and K. A. Rose. Individual-based model analysis of walleye and yellow perch population dynamics in response to changing ecosystem conditions. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Schultz, D. W., A. J. Carlson, S. Mortensen, and D. L. Pereira. 2013. Modeling population dynamics and fish consumption of a managed double-crested cormorant colony in Minnesota. North American Journal of Fisheries Management 33: 1283-1300.

Seefelt, N. E., and J. C. Gillingham. 2008. Bioenergetics and prey consumption of breeding double-crested cormorants in the Beaver Archipelago, northern Lake Michigan. Journal of Great Lakes Research 34: 122-133.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Tonn, W. M., C. A. Paszkowski, and I. J. Holopainen. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. Ecology 73: 951-958.

VanDeValk, A. J., C. M. Adams, L. G. Rudstam, J. L. Forney, T. E. Brooking, M. A. Gerken, B. P. Young, and J. T. Hooper. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 131: 27–39.

VanDeValk, A. J., L. G. Rudstam, J. R. Jackson, and S. D. Krueger. The Oneida Lake fishery: interactions between fishing and fish. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: longterm dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71: 2060-2068.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Wires, L. R. 2014. The double-crested cormorant: plight of a feathered pariah. Yale University Press, New Haven, Connecticut.

Wires, L. R., F. J. Cuthbert, D. R. Trexel, and A. R. Joshi. 2001. Status of the double-crested cormorant (*Phalacrocorax auritus*) in North America, final report to United States Fish and Wildlife Service. University of Minnesota, St. Paul.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology 81: 261-266.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends in Ecology & Evolution 16: 78-84.

Zhu, B., D. G. Fitzgerald, C. M. Mayer, L. G. Rudstam, and E. L. Mills. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. Ecosystems 9: 1017–1028.

CHAPTER 1

SPATIAL AND TEMPORAL COMPARISONS OF DOUBLE-CRESTED CORMORANT DIETS FOLLOWING THE ESTABLISHMENT OF ALEWIFE IN LAKE CHAMPLAIN, USA

This chapter has been reprinted with written permission from the Journal of Great Lakes Research and should be cited as:

DeBruyne, R. L., T. L. DeVault, A. E. Duerr, D. E. Capen, F. E. Pogmore, J. R. Jackson, and L. G. Rudstam. 2012. Spatial and temporal comparisons of double-crested cormorant diets following the establishment of alewife in Lake Champlain, USA. Journal of Great Lakes Research 38(Supplement 1): 123–130.

ABSTRACT

Increasing numbers of double-crested cormorants (*Phalacrocorax auritus*) on Lake Champlain have caused concerns related to potential impacts on the yellow perch (*Perca flavescens*) population. However, with the establishment of alewife (*Alosa pseudoharengus*) in 2003, cormorant foraging may have changed. We examined cormorant diets from four areas of Lake Champlain to assess past, current, and potential future impacts of cormorants on the changing fish community. During the breeding seasons of 2001-2002 and 2008-2009, we observed spatial and temporal differences in cormorant diets. Yellow perch dominated diet composition during 2001-2002 at Young Island (73% and 90% yearly weight totals) during all reproductive periods. Four Brothers Islands diet composition in 2002 varied according to reproductive period. In 2008 and 2009, alewife were predominant in diets at Four Brothers Islands (56% and 71%) and the South site (65% and 62%), with yellow perch comprising a high proportion of diets at Young Island (44% and 56%). Results from a MANOVA confirmed differences among sites, reproductive period, and the interaction of these factors (*P*

< 0.0001) when describing diet compositions for the post-alewife years. PCA results denoted a general shift in cormorant diets from 2001-2002 to 2008-2009. Our study demonstrated that the diet of piscivorous birds may shift with a new forage species and may vary significantly within a single large water body. Accordingly, efforts to manage piscivorous birds with the intent to decrease mortality of specific fish species should be site specific when possible.

INTRODUCTION

Double-crested cormorants (*Phalacrocorax auritus*; hereafter cormorants) are piscivorous, opportunistic predators that feed on a variety of fish species near their roosting areas and other nearby water bodies (Custer and Bunck 1992; Hatch and Weseloh 1999; Coleman et al. 2005; Seefelt and Gillingham 2006). On many lakes where cormorants have established nesting colonies, declines in resident sportfish populations, such as yellow perch (*Perca flavescens*) (Burnett et al. 2002; Rudstam et al. 2004; Fielder 2008, 2010), walleye (*Sander vitreus*) (Rudstam et al. 2004), and smallmouth bass (*Micropterus dolomieu*) (Lantry et al. 2002), have been observed. There are also concerns about cormorants feeding on newly stocked walleye and salmonids (Ross and Johnson 1999; Blackwell et al. 1997; Jensen 2001). As public pressure for cormorant management increases, a detailed assessment of cormorant feeding patterns is needed to guide effective management.

Like many other large lakes in the Midwest and Northeast, Lake Champlain has experienced increasing numbers of cormorants since the 1970s (Hatch 1995; Weseloh et al. 1995; Weseloh et al. 2002). Lake Champlain is located between the states of New York and Vermont, USA, and Quebec, Canada, and drains into the Richelieu River and eventually into the St. Lawrence River (Figure 1.1). Cormorants on Lake Champlain have been managed by federal and state agencies to minimize the destruction of vegetation and concomitant effects on co-nesting species. In 1999, an egg-oiling program was initiated on the Young Island colony (Grand Isle, VT) to reduce reproductive success and control population levels of

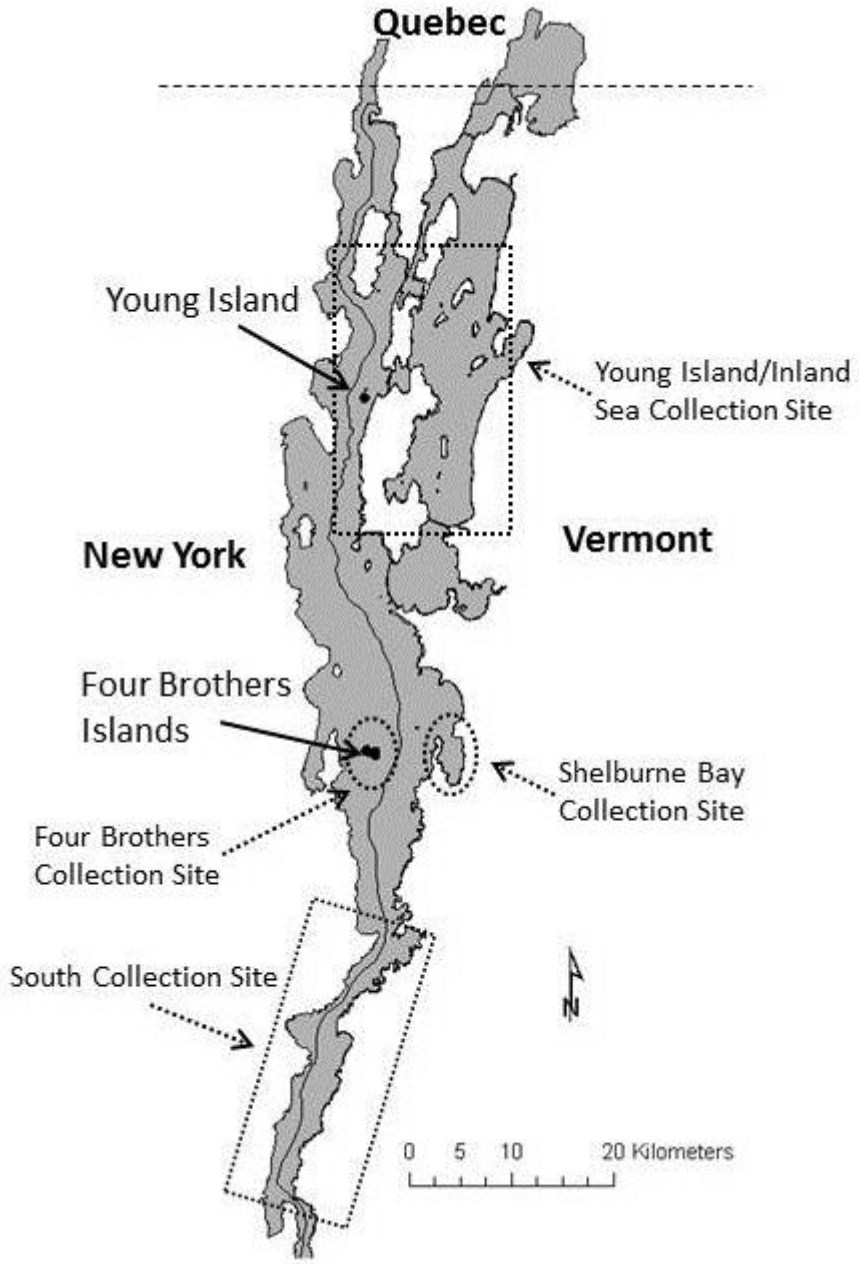


Figure 1.1. Map of Lake Champlain with the major cormorant colonies (Young and Four Brothers Islands) and collections sites (Four Brothers, Shelburne Bay, South, and Young Island/Inland Sea) labeled.

nesting cormorants. Management later included a culling program to more rapidly reduce cormorant numbers as a means of restoring native vegetation to the colony island. In the past decade, anglers have also expressed concerns about cormorant foraging on local sportfish populations, particularly yellow perch (John Gobeille, Vermont Fish and Wildlife Department, *personal communication*).

Cormorant impacts can vary across systems, and potential angler-cormorant conflicts should be addressed with system-specific information. Although cormorant impacts on sportfish populations have been documented in some systems (Rudstam et al. 2004; Fielder 2010; Dorr et al. 2010), studies on cormorant foraging habits in other locations have found that cormorants feed on fish and invertebrates not targeted by commercial fishermen or recreational anglers (Craven and Lev 1987; Ludwig et al. 1989; Seefelt and Gillingham 2006; Diana et al. 2006; Johnson et al. 2010). Neuman et al. (1997) compared cormorant diets from multiple sites in the Great Lakes region and found large variations spatially and temporally, suggesting that using diet data from one site to infer the impact of cormorants at another site is inappropriate. The contrasting results from studies assessing cormorant impacts on sportfish populations stress the need to base management on local conditions.

Changes in prey fish availability can result in changes in cormorant diets and potential impacts on fish communities. Smallmouth bass and yellow perch populations in eastern Lake Ontario were negatively affected by cormorants in the 1990s (Burnett et al. 2002; Lantry et al. 2002). However, since then, round goby (*Neogobius melanostomus*) has become established in eastern Lake Ontario and currently constitutes up to 93% of the diet (by number) of cormorants nesting on Little Galloo, Snake, and Pigeon Islands (Johnson et al. 2006, 2010). Therefore, the presence of round goby in cormorant diets should reduce cormorant foraging on previously impacted sportfish. Similar diet switches may occur in other areas where a new invasive fish becomes established, and therefore, the potential impacts of cormorants.

Alewife (*Alosa pseudoharengus*) were first observed in Lake Champlain in 2003 and

by 2007 had spread throughout the lake and are now reproducing naturally (Marsden and Hauser 2009). With the introduction of alewife to Lake Champlain, cormorants were presented with a new prey item as observed in the Great Lakes (Neuman et al. 1997; Seefelt and Gillingham 2006; Diana et al. 2006). This potential change in cormorant foraging pattern highlights the need for updated diet information in Lake Champlain.

Data regarding the diet composition of cormorants on Lake Champlain have been collected, but none after the establishment of alewife. Fowle (1997) collected undigested remains of fish regurgitated by cormorant chicks on Young Island in 1995 and 1996 and found that yellow perch represented more than 78% of the total regurgitate biomass collected each year; however, it was concluded that cormorants probably were not significantly affecting yellow perch populations. Because of increasing concerns about impacts of cormorants on fish populations in Lake Champlain and recent changes in the fish community, a comparison of the diet composition of cormorants before and after alewife establishment is important. Accordingly, the objectives of the present study were to (1) determine cormorant diet composition prior to and since alewife establishment by comparing diets in 2008-2009 to those from 2001-2002; and (2) investigate temporal and geographical differences in diet composition within a breeding season.

METHODS

Field Collection

Lake Champlain is located on the border between New York and Vermont, USA, and extends into Quebec, Canada (Figure 1.1). In 2001 and 2002, cormorants were followed from breeding colonies (Young Island and Four Brothers Islands) to foraging locations and collected with shotguns as they returned to the colony during four reproductive stages (incubation, nestling, fledgling, and post-breeding). During 2008 and 2009, cormorants were collected after foraging within the sampling locations or when returning to colonies from a

sampling location. The birds were collected with a shotgun during control operations conducted by Vermont Wildlife Services from four locations on Lake Champlain. These locations included the 'inland sea' and Young Island vicinity (YI); Shelburne Bay, east of Four Brothers Islands (SB); waters near Four Brothers Islands (FB); and the southern portion of the lake, south of Sloop Island (South). Collection sites varied such that SB and YI are generally shallower (<43m) with yellow perch and other warm-water fishes present; whereas FB and South areas are generally deeper (>43m) with alewife, emerald shiner (*Notropis atherinoides*), and rainbow smelt (*Osmerus mordax*) present. Collections were distributed over time such that approximately 20 birds were collected from each location during each of the four reproductive stages. Attention was given to collect birds which had likely already foraged; however, cormorants were not followed from the colonies and observed foraging before collection as they were in 2001 and 2002. In all years, cormorants, or their removed stomachs, were frozen and stored for later processing.

Diet evaluation

Cormorants, or cormorant stomachs, were thawed and the stomach contents extracted. Diet items were identified to the lowest possible taxon. Total, standard, or backbone length and/or scales were taken from diet items when possible to aid in assigning weights to prey items. Weights of diet items were determined using standard length-weight regressions (Schneider et al. 2000) except for yellow perch and rainbow smelt. Lake specific length-weight relationships were developed from yellow perch collected in 2001 and 2002 (M. Eisenhower and D. L. Parrish, *unpublished data*) and whole rainbow smelt removed from cormorant stomachs. For prey items that were too digested to obtain a length, lengths were assigned from either (1) the same species mean length from the same cormorant stomach (preferred method), (2) the same species and age based on scales (or young-of-year assigned age) collected from the same site and/or reproductive period, or (3) the mean length for that

species from the same site and/or reproductive period.

To determine if cormorant diets varied over time and space, diet compositions (proportion by weight) were tested among the collection sites and reproductive periods by year using a multivariate analysis of variance (MANOVA). We also included the interaction of collection site and reproductive period. The eight most frequently encountered diet items were retained as responses in the MANOVA (alewife, cyprinids, *Lepomis,* rainbow smelt, rock bass (*Ambloplites rupestris*), white perch (*Morone americana*), yellow perch, and other; see Table 1.2 for further details of species categories). There was some violation of independence between samples due to assigning mean length and weight to digested prey items; however, biases in results from this are likely minimal because assigned lengths were based on the same species and age from the same cormorant stomach when possible, and in most cases mean length was derived from the same site and period. Principal components analysis (PCA) was employed to visualize any shifts in cormorant diets before and after alewife established in Lake Champlain and what accounted for such shifts. The number of principal components retained in the analysis was determined according to latent root criterion. All components with Eigenvalues >1 were retained and remaining components underwent varimax rotation. Any violation of independence in the data as a result of using mean length and weight assigned to individual fish (from different cormorant stomachs) would not affect our ability to use PCA for the descriptive purposes of this study (McGarigal et al. 2000).

RESULTS

We collected 131 cormorants for diet analysis during the 2001-2002 seasons (Table 1.1). Diets included 3,119 identifiable prey items (3,249 total prey items) representing 21 species. The most common prey items identified during the pre-alewife period were yellow perch and rainbow smelt. Unidentified items accounted for 0.8-13.7% of prey items by number in a

Table 1.1. Number of cormorant stomach samples collected from sampling locations during each reproductive period on Lake Champlain containing identifiable stomach contents during the pre-alewife (2001-2002) and post-alewife (2008-2009) periods.

		Reproductive Period				
Year	**Collection Site**	**Incubation**	**Nestling**	**Fledgling**	**Post-Fledgling**	**Total**
2001	Young Island	5	35	16	12	68
2002	Four Brothers	10	12	3	2	27
	Young Island	7	14	8	7	36
2008	Four Brothers	20	19	17	17	73
	Shelburne Bay	2	15	2	18	37
	South	17	20	13	17	67
	Young Island	19	18	20	21	78
2009	Four Brothers	20	19	20	18	77
	Shelburne Bay	3	6	16	16	41
	South	20	17	20	20	77
	Young Island	15	17	20	16	68

single location and reproductive period (Table 1.2). Yellow perch accounted for 62-95% of consumption by weight for cormorants at Young Island during 2001 and 2002 during all reproductive periods (Figure 1.2). At Four Brothers Islands in 2002, rainbow smelt and other fish (e.g. cyprinids, *Lepomis*, and white perch) were the major contributors to cormorant diets, except during the incubation period, when yellow perch dominated the diet.

Five hundred eighteen cormorants were collected with stomach contents during the post-alewife period, 2008-2009 (Table 1.1). There were 5,728 identified prey items (5,754 total prey items) encompassing 26 species of fish (Table 1.2). Unidentified items accounted for 0-28.6% of prey items by numbers in a single location and reproductive period. Alewife constituted large proportions of cormorant diets at Four Brothers and South locations during incubation and nestling reproductive periods in 2008 and also during the fledgling period in 2009 (Figure 1.3). Rainbow smelt was the main diet item at Four Brothers and Shelburne Bay during the fledgling period and remained common in the diet at these locations during the post-fledgling period in 2008. Young Island cormorants consistently consumed yellow perch in high proportions, except during the nestling and fledgling periods in 2008 and the incubation period in 2009 when white perch was the most common diet item by weight. Shelburne Bay and Young Island displayed the highest variety of diet items consumed during 2008, with rock bass accounting for up to 25% of diet by weight.

When comparing pre- and post-alewife cormorant diets, alewife became a major component of cormorant diets at Four Brothers Islands. Alewife were the most common fish species in diets, comprising up to 98% (overall proportion 48%) of the prey items by number consumed at a single location and reproductive period (Table 1.2). Yellow perch, which were overall 14% of the identified prey items during the pre-alewife period, increased to 18% of the overall identified prey items at Four Brothers during the post-alewife period. Overall rainbow smelt frequency decreased from 74% during pre-alewife to 24% during the post-alewife period.

Table 1.2. Cormorant diet composition (% by number) from each sampling location during each of the four reproductive periods on Lake Champlain during pre-alewife (2001-2002) and post-alewife (2008-2009) time periods. site = sampling location; period = reproductive period; n = total number of items in diet.

Year	Site	Period	n	Alewife	Cyprinid[a]	*Lepomis* spp.[b]	Rainbow Smelt	Rock Bass	White Perch	Yellow Perch	Other[c]	Unidentified
2001	Young Island	Incubation	66	--	1.5	7.6	0.0	0.0	0.0	84.8	1.5	4.5
		Nestling	558	--	2.5	2.0	32.1	0.0	0.5	54.1	3.9	4.8
		Fledgling	175	--	6.9	5.1	0.6	0.6	0.6	71.4	6.9	8.0
		Post-Fledgling	749	--	11.6	0.3	74.6	0.0	0.0	12.4	0.3	0.8
2002	Four Brothers	Incubation	386	--	5.4	0.8	61.9	0.0	0.0	23.6	2.1	6.2
		Nestling	600	--	4.8	0.2	82.7	0.0	0.0	8.3	0.5	3.5
		Fledgling	24	--	0.0	0.0	66.7	0.0	0.0	25.0	4.2	4.2
		Post-Fledgling	86	--	8.1	1.2	72.1	0.0	4.7	4.7	4.7	4.7
	Young Island	Incubation	169	--	0.0	0.0	53.8	0.0	0.0	42.0	0.6	3.6
		Nestling	214	--	1.4	2.8	1.9	0.0	0.0	91.6	0.9	1.4
		Fledgling	120	--	3.3	3.3	0.8	0.0	0.0	81.7	5.0	5.8
		Post-Fledgling	102	--	2.0	2.0	0.0	0.0	26.5	54.9	1.0	13.7
2008	Four Brothers	Incubation	159	87.4	0.6	1.9	3.1	0.0	0.6	3.1	2.5	0.6
		Nestling	136	59.6	10.3	2.2	0.7	0.0	9.6	16.2	0.0	1.5
		Fledgling	384	0.5	0.0	0.0	98.4	0.0	0.0	0.8	0.0	0.3
		Post-Fledgling	446	54.7	1.3	0.0	25.8	0.9	0.0	16.1	0.4	0.7
	Shelburne Bay	Incubation	13	0.0	0.0	0.0	0.0	0.0	0.0	53.8	46.2	0.0
		Nestling	106	23.6	0.9	1.9	32.1	3.8	3.8	12.3	20.8	0.9
		Fledgling	7	0.0	0.0	0.0	71.4	0.0	0.0	0.0	0.0	28.6
		Post-Fledgling	209	32.5	2.9	0.5	56.9	2.9	0.5	2.4	1.4	0.0
	South	Incubation	165	95.8	0.6	0.0	1.8	0.0	0.0	0.6	1.2	0.0
		Nestling	170	75.9	10.0	1.8	0.0	0.0	2.4	8.8	1.2	0.0
		Fledgling	69	68.1	0.0	1.4	0.0	0.0	1.4	26.1	1.4	1.4
		Post-Fledgling	504	42.7	3.4	2.2	24.6	0.2	0.2	25.4	1.4	0.0
	Young Island	Incubation	103	4.9	5.8	5.8	34.0	0.0	1.9	39.8	2.9	4.9
		Nestling	40	2.5	2.5	2.5	0.0	0.0	42.5	42.5	0.0	7.5
		Fledgling	54	11.1	0.0	1.9	0.0	20.4	29.6	29.6	7.4	0.0
		Post-	325	90.8	0.9	0.0	0.3	0.3	0.3	6.2	0.9	0.3

Year	Site	Period	n	Alewife	Cyprinid[a]	*Lepomis* spp.[b]	Rainbow Smelt	Rock Bass	White Perch	Yellow Perch	Other[c]	Unidentified
		Fledgling										
2009	Four	Incubation	331	93.1	0.0	0.3	2.1	0.0	0.6	3.9	0.0	0.0
	Brothers	Nestling	281	79.4	0.0	1.1	2.8	0.0	0.4	16.4	0.0	0.0
		Fledgling	184	21.2	38.6	0.0	0.0	0.0	1.6	26.6	12.0	0.0
		Post-Fledgling	251	12.4	6.0	0.8	0.0	0.0	0.0	75.7	4.8	0.4
	Shelburne	Incubation	9	0.0	0.0	11.1	0.0	0.0	11.1	77.8	0.0	0.0
	Bay	Nestling	56	0.0	0.0	0.0	1.8	0.0	0.0	75.0	23.2	0.0
		Fledgling	312	6.4	53.2	0.0	13.5	0.0	0.6	10.9	15.4	0.0
		Post-Fledgling	194	29.4	1.5	1.0	17.5	0.5	0.0	48.5	1.5	0.0
	South	Incubation	407	98.5	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0
		Nestling	229	53.3	0.0	0.9	35.4	0.0	0.0	8.7	1.7	0.0
		Fledgling	191	47.1	28.8	0.0	15.2	0.0	0.5	5.2	3.1	0.0
		Post-Fledgling	113	2.7	16.8	4.4	0.0	3.5	1.8	65.5	4.4	0.9
	Young	Incubation	29	3.4	0.0	27.6	0.0	0.0	20.7	37.9	6.9	3.4
	Island	Nestling	83	30.1	8.4	4.8	0.0	0.0	7.2	45.8	2.4	1.2
		Fledgling	76	5.3	1.3	2.6	0.0	0.0	6.6	78.9	2.6	2.6
		Post-Fledgling	118	1.7	0.0	0.8	1.7	1.7	0.0	89.8	4.2	0.0

a includes bluntnose minnow (*Pimephales notatus*), emerald shiner (*Notropis atherinoides*), golden shiner (*Notemigonus crysoleucas*), spottail shiner (*Notropis hudsonius*), and unidentified minnow/shiner

b includes bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*)

c includes banded killifish (*Fundulus diaphanus*), black crappie (*Pomoxis nigromaculatus*), bowfin (*Amia calva*), bullhead (*Ameiurus* spp.), darter (*Etheostoma* spp.), fantail darter (*Etheostoma flabellare*), lake herring (*Coregonus artedi*), crayfish, *Esox* spp., largemouth bass (*Micropterus salmoides*), logperch (*Percina caprodes*), longnose dace (*Rhinichthys cataractae*), mottled sculpin (*Cottus bairdii*), sculpin (*Cottus* spp.), smallmouth bass (*Micropterus dolomieu*), tessellated darter (*Etheostoma olmstedi*), troutperch (*Percopsis omiscomaycus*), walleye (*Sander vitreus*), and white sucker (*Catostomus commersoni*)

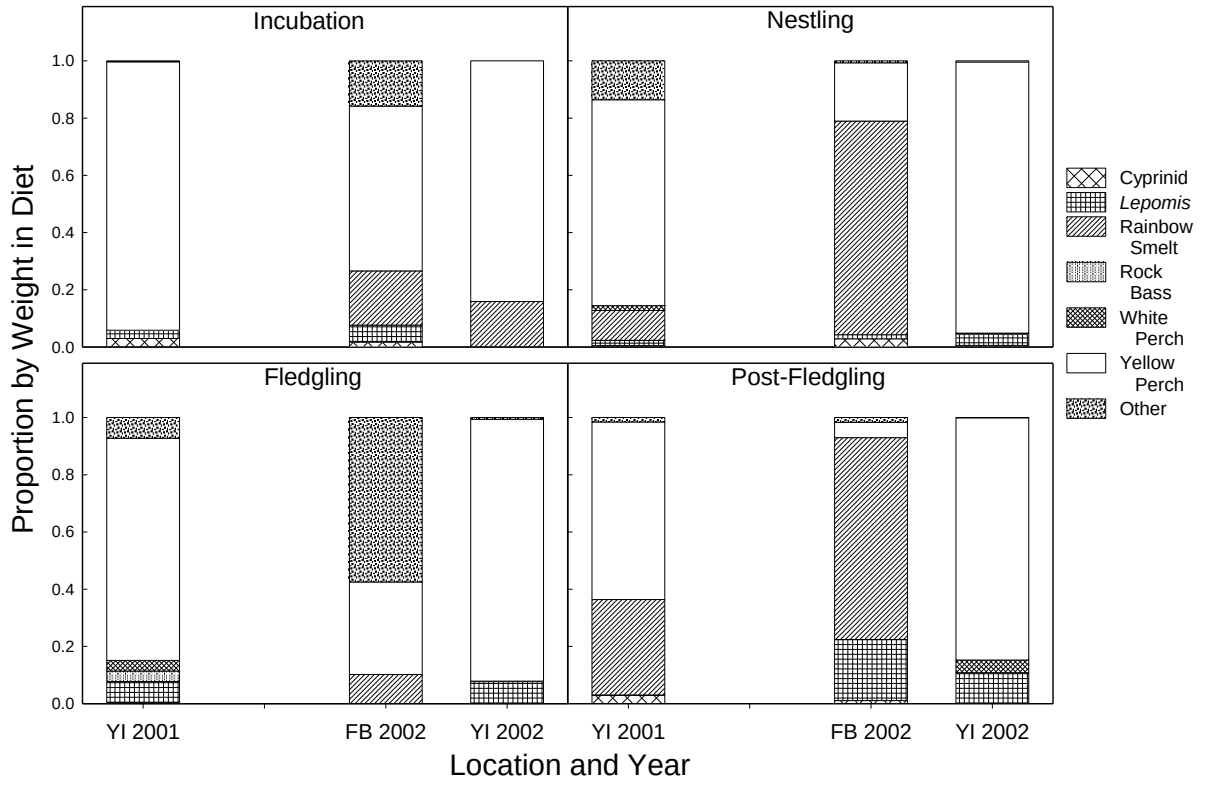


Figure 1.2. Cormorant diet composition by weight for identifiable items from Four Brothers Islands (FB) and Young Island (YI) during the 2001 and 2002 reproductive seasons on Lake Champlain. See Table 1.2 for a description of individual species included in cyprinid, *Lepomis*, and other categories. Note: 57% of total weight at Four Brothers during fledgling in 2002 was due to a single lake herring consumed.

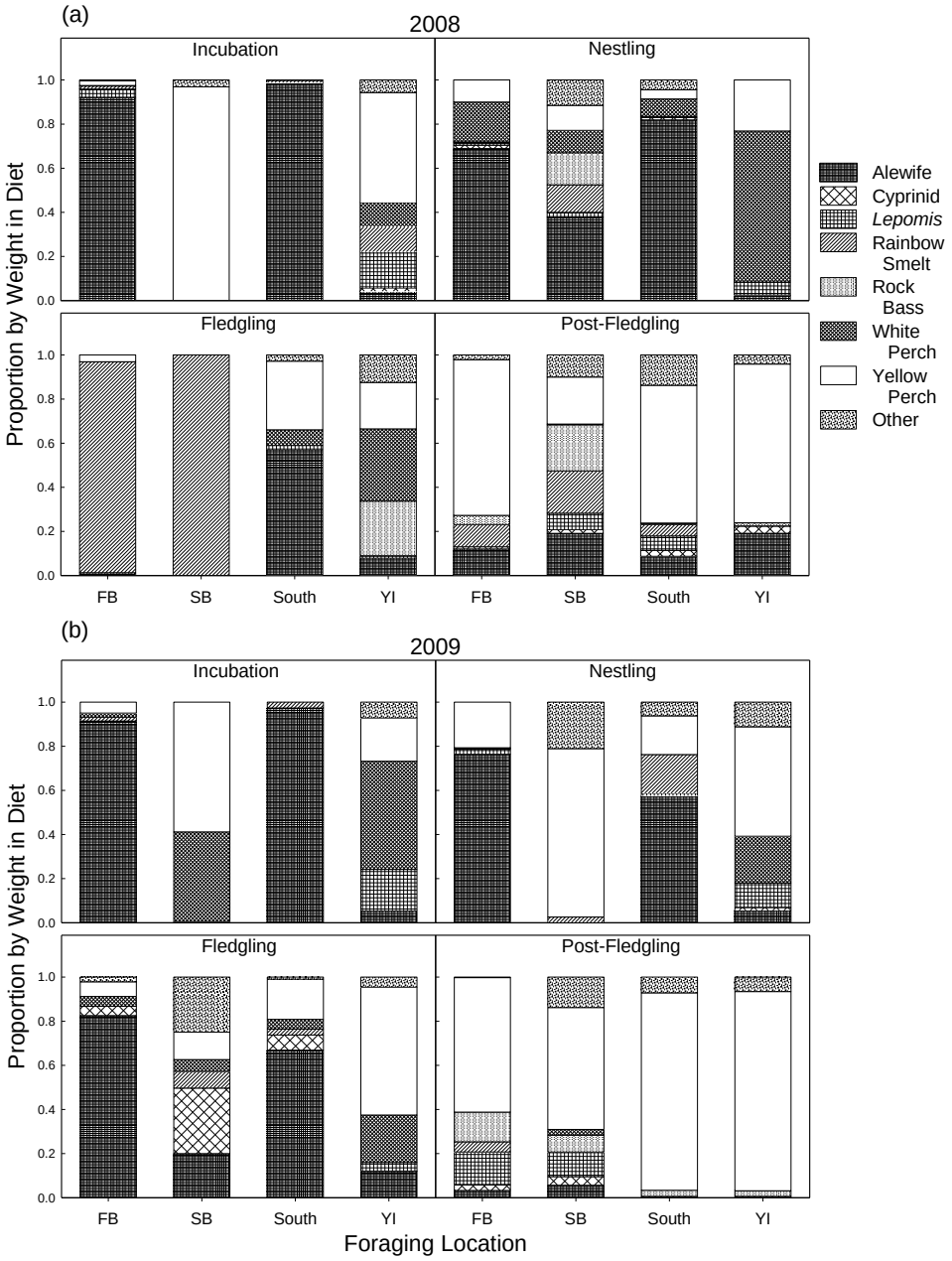


Figure 1.3. Cormorant diet composition by weight for identifiable items from Four Brothers Islands (FB), Shelburne Bay (SB), South, and Young Island (YI) during the 2008 (a) and 2009 (b) reproductive seasons on Lake Champlain. See Table 1.2 for a description of individual species included in cyprinid, *Lepomis*, and other categories.

Young Island cormorants continued to consume large numbers of yellow perch (overall pre-alewife 46% and post-alewife 38% of identified prey); however, there was an increase in the number of species consumed during the various reproductive stages between the pre- and post-alewife cormorant diets (Table 1.2). White perch were numerically important during the post-alewife period (6% of all diet items compared to 1% during the pre-alewife period). Rainbow smelt frequency decreased from pre- to post-alewife periods (39% to 5%), as did the numbers of unidentified prey items (8% to 2%). Alewife represented a high percentage of cormorant diets after their establishment (overall frequency 41%).

MANOVA results for pre-alewife years indicated no diet composition difference between reproductive periods at Young Island during 2001 ($P = 0.1$; $\alpha = 0.05$; Table 1.3). In 2002, statistical significance was found in the full model ($P = 0.04$) and between diets from Four Brothers and Young Island (site $P = 0.0037$). During the post-alewife period, site, reproductive period, and site*reproductive period interaction were significant effects when examining diet compositions for 2008 and 2009 (all $P < 0.0001$; Table 1.3). The full 2008 model accounted for 90% of the variation in the diet compositions and the full 2009 model accounted for 81% of the total variation in cormorant diet compositions (Table 1.3). Closer examination of species-specific trends at the four locations over time revealed alewife consumption generally decreased as the reproductive periods progressed at Four Brothers and South sites during 2008 and 2009 and remained low during all reproductive periods at Shelburne Bay and Young Island during 2008 and 2009, with the exception of the post-fledgling period at Young Island in 2008 (Figure 1.4). Cormorant consumption of rainbow smelt increased at Four Brothers and Shelburne Bay during the fledgling and post-fledgling periods in 2008; however, no increase in rainbow smelt contribution over time was evident during 2009 at any location. In 2008 and 2009, white perch were consumed in low proportions at all locations except Young Island, where their contribution varied among periods. Yellow perch consumption was consistently higher at Young Island and Shelburne

Table 1.3. Results from the MANOVA for 2001-2002 and 2008-2009 testing for differences among the four reproductive periods (incubation, nestling, fledgling, and post-fledgling) and collection sites (Four Brothers, Shelburne Bay, South, and Young Island). The MANOVA independent variables were the eight major species in diet as percent composition by weight. Note: 2001 included only Young Island and 2002 included only Young Island and Four Brothers. See Figure 1.4 for species categories and individual trends for species in cormorant diets in 2008 and 2009.

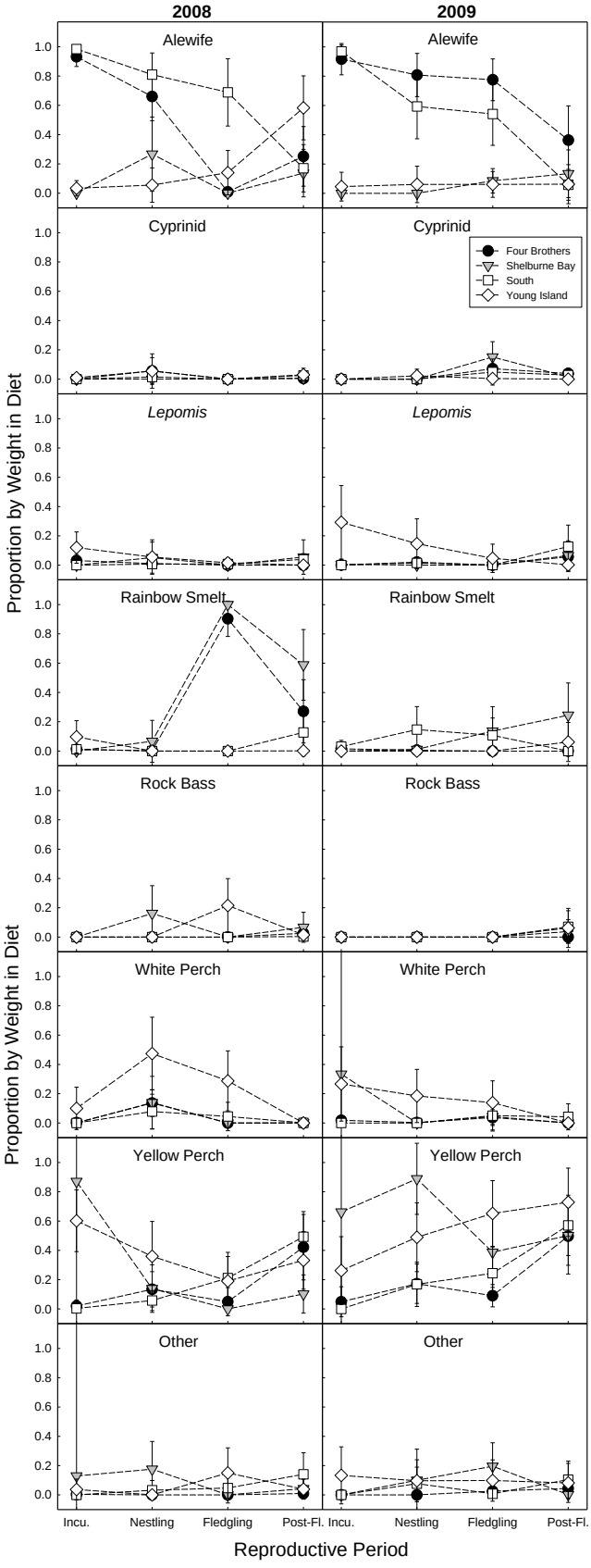
Year	Factor	Wilks' λ	df (num, dem)	F	*P*
2001	Full Model[a]	0.5827	24, 165.92	1.41	0.11
	Intercept		8, 57	146.39*	<0.0001
2002	Full Model	0.2522	56, 269.18	1.40	0.04
	Intercept		8, 49	223.36*	<0.0001
	Site	0.5499[b]	8, 49	3.37*	0.0037
	Period	0.6494	24, 142.72	0.95	0.53
	Site*Period	0.6572	24, 142.72	0.93	0.57
2008	Full Model	0.0968	120, 1664	5.38	<0.0001
	Intercept		8, 232	504.60*	<0.0001
	Site	0.4553	24, 673.47	8.74	<0.0001
	Period	0.5677	24, 673.47	6.05	<0.0001
	Site*Period	0.2766	72, 1418.8	4.63	<0.0001
2009	Full Model	0.1917	120, 1720.9	3.74	<0.0001
	Intercept		8, 240	579.70*	<0.0001
	Site	0.4415	24, 696.67	9.45	<0.0001
	Period	0.7220	24, 696.67	3.45	<0.0001
	Site*Period	0.5501	72, 1467.4	2.10	<0.0001

* exact F

[a] 2001 full model only includes the factor Period

[b] F-test value

Figure 1.4. Mean proportion by weight for identified species in cormorant diets in 2008 and 2009 during each reproductive period (incubation [Incu.], nestling, fledgling, post-fledgling [Post-Fl.]) from Four Brothers, Shelburne Bay, South, and Young Island collection sites in Lake Champlain with 95% confidence intervals around means. See Table 1.2 for a description of individual species included in cyprinid, *Lepomis*, and other categories.


2008
2009
Alewife
Cyprinid
Lepomis
Rainbow Smelt
Rock Bass
White Perch
Yellow Perch
Other
Four Brothers
Shelburne Bay
South
Young Island
Proportion by Weight in Diet
Incu.
Nestling
Fledgling
Post-Fl.
Reproductive Period

Bay than Four Brothers and South sites during 2008 and 2009 during most reproductive periods. Consumption of yellow perch at Four Brothers and South locations generally increased as the reproductive season progressed in 2008 and 2009. Consumption of other fish species was generally low, but variable, at all locations during both years over time.

Six components were retained in the PCA analysis based on latent root criterion, and accounted for 88% of the total variation (Table 1.4). The first two axes explained only 20% and 15% of the variation in this diet compositional data. The remaining axes explained approximately 13%-14% of the variation. The first principal component was strongly influenced by yellow perch (principal component loading 0.89) and alewife (-0.88). The second principal component was heavily influenced by rainbow smelt (0.99); as well as yellow perch (-0.31) and alewife (-0.30). Despite relatively even distribution of variance among the six components, diet compositions are distinguishable between pre- and post-alewife periods based on the first two principal components (Figure 1.5).

DISCUSSION

It is clear from this study that alewife have become a dominant food item for double-crested cormorants feeding in Lake Champlain. Cormorant diets were comprised of >98% alewife, especially when foraging near Four Brothers Islands and in the southern portion of the lake. Although no single principal component accounted for >20% of the variation when explaining these diet data, a shift in the cormorant diet composition after alewife became established was still evident, in particular at the Four Brothers location. The incorporation of alewife into cormorant diets from four large and distinct areas on Lake Champlain confirms that alewife are an important food item, and with continued availability, may remain important in the diets. However, cormorants continued to rely on yellow perch, especially near Young Island. Rainbow smelt also remained seasonally important in the diets of cormorants foraging around Four Brothers Islands and Shelburne Bay. Lack of difference in diet composition between

Table 1.4. Principal component loadings for the cormorant diet composition (% by weight) input data when retaining six principal components based on latent root criterion. Loadings >|0.3| are bolded. See Table 1.2 for species contained in cyprinid, *Lepomis*, and other categories.

Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Alewife	**-0.88**	**-0.30**	-0.22	-0.20	-0.15	-0.16
Cyprinid	0.01	-0.03	**0.73**	-0.01	**-0.34**	0.09
Lepomis	0.02	-0.04	-0.02	-0.03	0.02	**0.99**
Rainbow Smelt	-0.01	**0.99**	-0.07	-0.06	-0.04	-0.04
Rock Bass	0.00	-0.03	-0.01	-0.01	**0.88**	0.04
White Perch	-0.01	-0.05	-0.05	**1.00**	-0.02	-0.03
Yellow Perch	**0.89**	**-0.31**	-0.17	-0.22	-0.15	-0.13
Other	0.02	-0.04	**0.72**	-0.05	**0.36**	-0.11
% of variance	19.5	14.8	14.1	13.6	13.3	13.1
Cumulative %	19.5	34.3	48.4	62.0	75.3	88.4

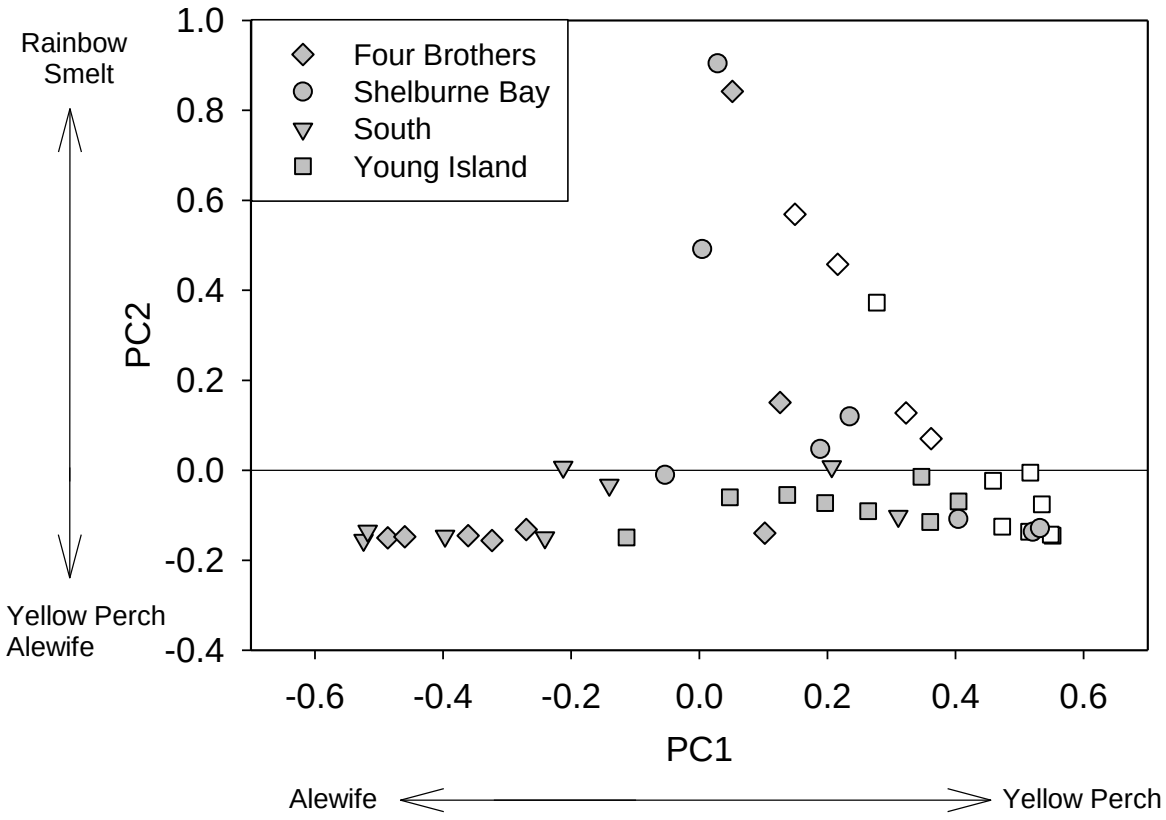


Figure 1.5. Biplot ordination of the first two principal components explained by cormorant diet composition (% by weight) on Lake Champlain. Open symbols represent specific site-reproductive period values during pre-alewife years (2001-2002) and shaded symbols represent post-alewife years (2008-2009). Percent yellow perch (principal component loading 0.89) and alewife (-0.88) in the diets influenced the first axis. Percent rainbow smelt (0.99) in the diets strongly influence the second axis. See Table 1.4 for complete list of principal component loadings.

reproductive stages during the pre-alewife period may be due to limited sample sizes. It may also be partially due to the diet samples being summarized by colony location, instead of foraging location; cormorants from Four Brothers colony forage throughout Lake Champlain (Duerr et al. 2012). By sampling according to foraging location, potential localized effects of cormorants on fish species can be better determined.

When round goby became established in eastern Lake Ontario, cormorant diets reflected this change almost immediately and round goby became dominate in the diet (Johnson et al. 2006, 2010). Although this study did not monitor cormorant diets simultaneously with the establishment of alewife, within five years of the alewife introduction this species became a dominant diet item for cormorants on Lake Champlain in at least two foraging locations, Four Brothers Islands and in the southern section of the lake. This suggests that some cormorants in Lake Champlain have switched their mode of feeding from demersal on yellow perch to pelagic foraging on alewife. This switch in foraging mode also has a geographic component. Cormorants still forage on yellow perch near Young Island; however, cormorants from the Four Brothers colony, currently the largest nesting colony on the lake and the only one where a substantial number of young are produced, may be able to capitalize on the regular food resources in nearby pelagic zones of the lake. From 2002 to 2003, cormorants from Four Brothers shifted away from pelagic foraging locations close to the breeding site, where they predominately consumed rainbow smelt in 2002, to more distant littoral locations in 2003 (Duerr et al. 2012). An associated increase in energy demand accompanied this shift in foraging distribution (Duerr et al. 2012). Thus, reduced energetic demands associated with alewife as a regular food supply near the Four Brothers Islands may have potential to increase cormorant reproductive output at the Four Brothers colony.

Even though alewife have become an important and sometimes dominant component of cormorant diets on Lake Champlain, effects of cormorant predation on yellow perch are still unknown. Significant negative effects on smallmouth bass populations were found in

eastern Lake Ontario when smallmouth bass only comprised 0.8%-7.2% of the diet of cormorants (Johnson et al. 2002; Lantry et al. 2002). On Oneida Lake, in central New York, cormorant diets consisted of 1.6%-16.5% subadult walleye and 33.3%-64.7% subadult yellow perch and this consumption level was large enough to reduce walleye and yellow perch populations significantly (Rudstam et al. 2004). In contrast to the negative impact cormorants had on yellow perch in Oneida Lake (Rudstam et al. 2004), a previous study conducted on Lake Champlain, based on gillnet catches of yellow perch through the cormorant reproductive season, indicated that cormorants were likely not negatively affecting the yellow perch population around Young Island (Eisenhower and Parrish 2009). Assuming that the cormorant population on Lake Champlain remains stable, the presence of alewife could lessen any negative effects cormorants exert on the yellow perch population. However, without information on the yellow perch population, such as population estimates, growth and/or mortality trends, we still are unable to ascertain the actual impact cormorants have on yellow perch.

Researchers in other areas have suggested that alewife might reduce cormorant predation on yellow perch by acting as a buffer (O'Gorman and Burnett 2001; Diana et al. 2006). Observed differences in diets of cormorants during the post-fledgling period between 2008 and 2009 could provide additional corroboration. In 2008, young-of-year alewife and rainbow smelt numerically dominated diets at all locations (combined 67%-91% of fish species consumed) during the post-fledgling period. In 2009, young-of-year alewife and rainbow smelt were not predominant in the diet and even absent in some locations in the post-fledgling period. Instead, 2009 post-fledgling diets were predominately yellow perch (48%-90% of fish species consumed). One reason for this shift in the post-fledgling period would be the availability of young-of-year rainbow smelt and alewife. In 2008, the average catch of young-of-year rainbow smelt and alewife in index trawls was 1003 and 523 individual fish; however, the catches dropped dramatically in 2009 to 264 and 106 individuals at the same

standard sites (Staats and Pientka 2010). The ability of cormorants to forage effectively when alewife and rainbow smelt are scarce illustrates their capacity for adapting to changing prey populations. Adaptive foraging by cormorants, spatially and within and between years, also indicated that spatially and temporally limited diet studies may miss important information for evaluating potential impacts of cormorants.

Continued management of cormorants on Lake Champlain should reflect the current understanding of their effects on the ecosystem and established conservation and management goals. Currently no cormorant reproduction is permitted on Young Island and nesting is restricted on Four Brothers Islands with the goal of reducing negative impacts on native vegetation and co-nesting species. Results from this study support the view that management of cormorants should be site specific, potentially even within a single water body, if the rationale for management actions includes reducing predation pressure by cormorants on fish species such as yellow perch in Lake Champlain. We found cormorant diets to vary significantly across geographic locations and reproductive stages and have changed composition in response to alewife and rainbow smelt availability. There also should be efforts undertaken to assess population parameters of the fish species in question, such as population and mortality levels, which when implementing cormorant control should be monitored and assessed for changes. Without proper baseline data and continued monitoring, management efforts cannot be implemented most effectively to achieve the desired results.

ACKNOWLEDGEMENTS

This research was funded in part by the U.S. Department of Agriculture, Wildlife Services programs in New York and Vermont, a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, US Department of Commerce, to Lake Champlain Sea Grant under grant number NA16RG2206. Funding also was provided by a Kieckhefer Adirondack Fellowship, Vermont Department of Fish and Wildlife, The Jack H.

Berryman Institute, and U.S. Fish and Wildlife Service. We are grateful to M. D. Eisenhower, Q.L. Chen and K.J. Wu for time spent processing cormorants and laboratory work, as well as T. Donovan and D. Parrish for additional support. We thank personnel from Vermont Fish Wildlife Services, New York Wildlife Services, Vermont Department of Fish and Wildlife, New York Department of Environmental Conservation, Adirondack Chapter of The Nature Conservancy, and Missisquoi National Wildlife Refuge for cooperating in numerous ways, and J. McConnell and M. Lowney for logistical support. B. Dorr and three anonymous reviewers provided comments that improved this manuscript. Use of trade-names in this article does not imply endorsement by the federal government. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. Geological Survey, Vermont Department of Fish and Wildlife, the University of Vermont, and the Wildlife Management Institute. This is contribution 280 from the Cornell Biological Field Station.

LITERATURE CITED

Blackwell, B.F., W.B. Krohn, N.R. Dube, and A.J. Godin. 1997. Spring prey use by double-crested cormorants on the Penobscot River, Maine, U.S.A. Colonial Waterbirds 20: 77-86.

Burnett, J.A., N.A. Ringler, B.F. Lantry, and J.H. Johnson. 2002. Double-crested cormorant predation on yellow perch in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 202-211.

Coleman, J.T.H., M.E. Richmond, L.G. Rudstam, and P.M. Mattison. 2005. Foraging location and site fidelity of the double-crested cormorant on Oneida Lake, New York. Waterbirds 28: 498-510.

Craven, S.R., and E. Lev. 1987. Double-crested cormorants in the Apostle Islands, Wisconsin, USA: population trends, food habits, and fishery depredations. Colonial Waterbirds 10: 64-71.

Custer, T.W., and C. Bunck. 1992. Feeding flights of breeding double-crested cormorants at two Wisconsin colonies. Journal of Field Ornithology 63: 203-211.

Diana, J.S., S. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32: 306-320.

Dorr, B.S., A. Moerke, M. Bur, C. Bassett, T. Aderman, D. Traynor, R. Singleton, P. Butchko, and J.D. Taylor II. 2010. Evaluation of harassment of migrating double-crested cormorants to limit depredation on selected sport fisheries in Michigan. Journal of Great Lakes Research 36: 213-223.

Duerr, A.E., D.E. Capen, and T.M. Donovan. 2012. Energetic considerations for managing double-crested cormorants on Lake Champlain. Journal of Great Lakes Research 38(Supplement 1): 131-140.

Eisenhower, M.D., and D.L. Parrish. 2009. Double-crested cormorant and fish interactions in a shallow basin of Lake Champlain. Waterbirds 32: 388-399.

Fielder, D.G. 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of double-crested cormorants. Journal of Great Lakes Research 34: 506-523.

Fielder, D.G. 2010. Response of yellow perch in Les Cheneaux Islands, Lake Huron to declining numbers of double-crested cormorants stemming from control activities. Journal of Great Lakes Research 36: 207-214.

Fowle, M.R. 1997. Population dynamics, food habits, and bioenergetics of double-crested cormorants in Lake Champlain. M.Sc. Thesis, University of Vermont, Burlington, VT.

Hatch, J.J. 1995. Changing populations of double-crested cormorants. Colonial Waterbirds 18 (Special Publications 1): 8-24.

Hatch, J.J., and D.V. Weseloh. 1999. Double-crested cormorant (*Phalacrocorax auritus*), in: Poole, A., Gill, F. (Eds.), The birds of North America, No. 441. Inc., Philadelphia, Pennsylvania.

Jensen, A.L. 2001. Modelling the effect of cormorant predation on stocked walleye. Ecological Modelling 145:123-127.

Johnson, J.H., R.M. Ross, and R.D. McCullough. 2002. Little Galloo Island, Lake Ontario: A review of nine years of double-crested cormorant diet and fish consumption information. Journal of Great Lakes Research 28: 182–192.

Johnson, J.H., R.M. Ross, R.D. McCullough, and B. Boyer. 2006. Diet composition and fish consumption of double-crested cormorants from the Little Galloo Island colony of eastern Lake Ontario in 2005. in: NYSDEC Annual Report 2005, Section 14, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.

Johnson, J.H., R.M. Ross, R.D. McCullough, and A. Mathers. 2010. Diet shift of double-crested cormorants in eastern Lake Ontario associated with the expansion of the invasive round goby. Journal of Great Lakes Research 36: 242-247

O'Gorman, R., and J.A.D. Burnett. 2001. Fish community dynamics in northeastern Lake Ontario with emphasis on the growth and reproductive success of yellow perch (*Perca flavescens*) and white perch (*Morone americana*), 1978 to 1997. Journal of Great Lakes Research 27: 367–383.

Lantry, B.F., T.H. Eckert, C.P. Schneider, and J.R. Chrisman. 2002. The relationship between abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 193-201.

Ludwig, J.P., C.N. Hill, M.E. Ludwig, and H.J. Auman. 1989. Food habits and feeding ecology of nesting double-crested cormorants in the upper Great Lakes, 1986-1989. Jack-Pine Warbler 67: 115-126.

Marsden, J.E., and M. Hauser. 2009. Exotic species in Lake Champlain. Journal of Great Lakes Research 35: 250-265.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag New York, Inc., New York.

Neuman, J., D.L. Pearl, P.J. Ewins, R. Black, D.V. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54: 1569–1584.

Ross, R.M., and J.H. Johnson. 1999. Fish losses to double-crested cormorant predation in eastern Lake Ontario, 1992-97. Pp. 61-70 in M. E. Tobin (Tech. Ed.). Symposium on double-crested cormorants: population status and management issues in the Midwest (9 December 1997, Milwaukee, WI). U.S. Department of Agriculture Technical Bulletin No. 1879.

Rudstam, L.G., A.J. VanDeValk, C.M. Adams, J.T.H. Coleman, J.J. Forney, and M.E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14: 149-163.

Schneider, J.C., P.W. Laarman, and H. Gowing. 2000. Chapter 17: Length-Weight Relationships. Manual of Fisheries Survey Methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.

Seefelt, N.E., and J.C. Gillingham. 2006. A comparison of three methods to investigate the diet of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, northern Lake Michigan. Hydrobiologia 567: 57-67.

Staats, N.R., and B. Pientka. 2010. Forage fish monitoring. Federal Aid Job Performance Report F- 35-R-12, Job 1. Vermont Fish and Wildlife Department, Waterbury, Vermont.

Weseloh, D.V., P.J. Ewins, J. Struger, P. Mineau, C.A. Bishop, S. Postupalsky, and J.P. Ludwig. 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 and 1991. Colonial Waterbirds 18 (Special Publication 1): 48-59.

Weseloh, D.V., C. Pekarik, R. Havelka, G. Barrett, and J. Reid. 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas 1990-2000: a manager's guide. Journal of Great Lakes Research 28:125-144.

CHAPTER 2

ANALYSIS OF PREY SELECTION BY DOUBLE-CRESTED CORMORANTS: A 15-YEAR DIET STUDY IN ONEIDA LAKE, NEW YORK

This chapter has been reprinted with written permission from the journal Transactions of the American Fisheries Society and should be cited as:

DeBruyne, R. L., J. T. H. Coleman, J. R. Jackson, L. G. Rudstam, and A. J. VanDeValk. 2013. Analysis of prey selection by double-crested cormorants: a 15-year diet study in Oneida Lake, New York. Transactions of the American Fisheries Society 142: 430-446.

ABSTRACT

Piscivorous birds, in particular cormorants *Phalacrocorax* spp., have been reported to cause declines in some fish populations in both Europe and North America, but not in others. This difference may be due to prey selection by cormorants that is further dependent on the composition of the fish assemblage present. We present 15 years of diet data collected Oneida Lake, NY, where we have previously documented negative effects of double-crested cormorants *Phalacrocorax auritus* on two fish populations valued by anglers: walleye *Sander vitreus* and yellow perch *Perca flavescens*. The Oneida Lake fish community changed through the study period and this change was reflected in cormorant diet samples. Diet samples were variable based on season and year with emerald shiner *Notropis atherinoides*, gizzard shad *Dorosoma cepedianum*, *Lepomis* spp., logperch *Percina caprodes*, walleye, and yellow perch having the highest overall relative importance. In years when age-0 gizzard shad were abundant they dominated double-crested cormorant diets in the fall after shad reached a length of 45mm. Consumption of emerald shiner and gizzard shad was positively related to each species' abundance, but no significant correlation between availability and consumption was found for walleye, white perch *Morone americana*, or yellow perch. Double-crested cormorants may be displaying prey switching behavior and selecting for

smaller, soft-rayed prey species. We conclude that variation in fish recruitment influences double-crested cormorant food selection habits and highlight the importance of continued monitoring with changing fish communities to reliably assess potential impacts of cormorants on a fish community over time.

INTRODUCTION

Predator-prey interactions are central to the dynamics of food webs and ecosystems. Diet studies reveal the structure of the food web and how species interact within a community (Polis 1991; Wooten 1997; Harvey et al. 2003). Diet studies, coupled with estimates of abundance of available prey species, can indicate if and how predators select prey; information essential for understanding the dynamics of predator-prey systems with multiple potential prey species (Wilbur and Fauth 1990; Hansson et al. 2007). Diet studies conducted over a brief time period may not reveal the full range of predator behavior, especially when prey composition varies over time. Piscivorous waterbirds, such as double-crested cormorants *Phalacrocorax auritus* (hereafter cormorants), are top predators in many aquatic systems and several studies have demonstrated that they can impact prey populations (e.g., Lantry et al. 2002; Burnett et al. 2002; Steinmetz et al. 2003; Rudstam et al. 2004; Fielder 2008). However, impacts to prey populations have not been detected in many systems (e.g., Craven and Lev 1987; Ludwig et al. 1989; Neuman et al. 1997; Diana et al. 2006; Dalton et al. 2009). The degree of potential cormorant impacts may depend on a number of conditions, including the quantity of cormorants foraging pressure, the composition of the prey assemblage, and patterns of prey selection exhibited by cormorants. Fish community structure and prey selection will therefore affect the degree of impact of cormorant predation on sport fisheries. Demonstrating preference for specific prey species, or prey groups, may aid in predicting cormorant impacts on local fish communities and clarify our understanding of cormorant foraging behavior.

Variability in cormorant diets among locations and across time has led to their characterization as generalist predator consuming prey in the same frequency as encountered within the environment (Lewis 1929; Ludwig et al. 1989; Neuman et al. 1997; Johnson et al. 2010). However, variability in diet composition alone does not verify that cormorants are not selective predators. Detailed studies of cormorant feeding selectivity are rare because they require comparison of diets with quantitative estimates of prey abundance which is seldom available (but see Rudstam et al. 2004; Diana et al. 2006; Dalton et al. 2009). In addition, prey switching (predators disproportionately consuming alternative prey when original prey becomes rare relative to the alternative prey) may be investigated by comparing cormorant diets in years with contrasting prey fish abundance (Murdoch 1969). Prey switching can stabilize predator-prey interactions by reducing the magnitude of prey abundance fluctuations and be more complete if different prey require different foraging tactics (Murdoch 1969; Oaten and Murdoch 1975). For example, cormorants may show differential preference between feeding on open-water schooling fish like gizzard shad *Dorosoma cepedianum* or emerald shiners *Notropis atherinoides*, compared to benthic fish species such as yellow perch *Perca flavescens* and round goby *Neogobius melanostomus*. Long-term studies of cormorant diets in conjunction with information on fish community structure are rare but highly valuable for detailed characterization of the foraging behavior of this controversial piscivore. One location with long-term quantitative information on both cormorant diets and fish community composition with abundance estimates is Oneida Lake, New York.

The objectives of this study were to examine double-crested cormorant diet composition and evaluate the extent to which diets reflect changes in the fish community. We investigated whether cormorant diets and prey selection varied by season (spring-summer compared to late-summer-fall), year, and in response to changes in the fish community using 15 years of cormorant diet and fish abundance data from Oneida Lake, New York (1995-2009). We report the overall composition of cormorant diets, statistical evaluations of diet

patterns, and prey selectivity of cormorants. Because cormorants have been implicated in the decline of walleye *Sander vitreus* and yellow perch populations, the two main species sought by anglers in Oneida Lake (Rudstam et al. 2004; VanDeValk et al., in press), we were particularly interested in how cormorant consumption of these species was affected by their abundance and the presence of alternative prey species such as gizzard shad and emerald shiner.

STUDY AREA

Oneida Lake is a shallow, moderately productive lake with a surface area of 207 km^2 (Mills et al. 1978). Oneida Lake is the largest lake contained entirely within the State of New York and has a valuable recreational fishery for walleye, yellow perch, smallmouth bass *Micropterus dolomieu* and largemouth bass *M. salmoides* (Connelly and Brown 1991; VanDeValk et al., in press). Zebra mussels *Dreissena polymorpha* were discovered in the lake in 1991 and quagga mussels *D. bugensis* arrived around 2005 (Mills et al., in press). The colonization of the lake by zebra mussels was followed by increasing water clarity and an increase in macrophyte coverage (Zhu et al. 2006); however no decrease in primary production was observed (Idrisi et al. 2001). Cormorants first nested on Oneida Lake in 1984 (Claypoole 1988). Nest counts increased steadily from 1984, peaking at 365 nests in 2000 (Coleman 2009). Migrating cormorants also stop-over on Oneida Lake, typically arriving in August and remaining on the lake through October. Total daily abundance increased over time and was found to exceed 2000 in 1996 and 1997 (Rudstam et al. 2004; Coleman 2009). Cormorant management was initiated in 1991 with a series of progressively more restrictive management actions enacted through 2009 (Coleman 2009). From 1991-1997, management largely focused on restricting nesting locations to specific island locations on the lake. Control actions were escalated from 1998-2003 when the colony was limited to 100 active nests through nest destruction and egg oiling, coupled with non-lethal harassment program

designed to move all cormorants off of the lake starting around 01September. Beginning in 2004, cormorant management consisted of non-lethal harassment through the entire breeding and migration seasons (April-September/October), along with nest destruction and egg oiling of all nests on the lake (DeVault et al. 2012).

METHODS

The fish community in Oneida Lake has been sampled annually since 1955 using gillnets and bottom trawls, and with hydroacoustics sampling starting in 1994. The same standardized methods were used each year, although acoustic units were replaced over time (details in Irwin et al. 2008). Gillnets were set in 15 standard locations, one location each week for 15 weeks (June-September) in the same order each year to sample subadult and adult fishes. Bottom trawls were conducted weekly at 10 standard sites (July-October) to estimate age-0 and juvenile fish densities. Mark-recapture population estimates have been conducted every second year for walleye and five non-consecutive years for yellow perch since 1995 (methods in Rudstam et al. 2004). Annual densities of subadult and adult walleye and yellow perch were estimated using a combination of mark-recapture estimates, gillnet and trawl catch (Irwin et al. 2008; Rudstam and Jackson 2011; Jackson et al. 2010). White perch *Morone americana* gillnet catch (number/year) was used as a proxy for population density.

Gizzard shad and emerald shiner abundances were estimated annually using hydroacoustics complemented with mid-water trawls, and vertical small-mesh gillnets in late August/early September. Surveys were conducted using a 70 kHz (1995-2004, Simrad EY500, 11.4° beam width) or a 120/123 kHz split beam unit (2005-2009, Biosonics DT-X, 7.2/7.8° beam width). Acoustic data were analyzed with EchoView (v4.7). All densities were calculated from *in situ* backscattering cross section (average for target strengths larger than –60dB) and echo integration according to the standard operating procedure for Great Lakes acoustics (Parker-Stetter et al. 2009). Abundance was based on using each transect as a

cluster of 500 m long elementary sampling units (Scheaffer et al. 2006).

Gizzard shad and emerald shiner were sampled in association with acoustic surveys using a mid-water fry trawl and fine-mesh gillnets described in Jackson et al. (2010). These gears were used to assess the species composition of young fish in the pelagic zone. Two trawl hauls were completed at each of 10 sites, and fish were preserved in formalin and returned to the lab for species identification, enumeration, and measurement. Fine-mesh gillnets, 21 m long, were set either on bottom or suspended from the surface. Paired (1 surface and 1 bottom) gillnets were set at each of 4 deep stations, and 4 shallow stations were sampled with only 1 net that sampled the entire water column.

Acoustic density estimates were apportioned to emerald shiner, gizzard shad, and other fish based on catches in vertical gillnets and mid-water trawls after accounting for the relative length selectivity and effort of the two gears. Fish in the top 2 m of the water column were accounted for by calculating the average density of gizzard shad and emerald shiner caught in the top 2 m in vertical gillnets set and midwater trawl samples (see Rudstam et al. 2011).

For this study we used cormorant diet information collected from 1995-2009. Cormorant diets were first sampled in 1988 using chick regurgitant at the nesting colonies. Chick and adult regurgitant samples were collected in 1995-1996, and 1998-2003, pellets were collected in 1997, and whole birds (stomachs) were collected in 1995-1996 and 2001-2009. Samples were collected from April-October, but specific sampling schedules varied by year. For analyses, samples were classified into two seasons, ‘summer’ (April-July) and ‘fall’ (August-October). Limited spring samples (April-May) were combined with summer samples because of low sample size in the spring and similarities in species and sizes present with summer diet composition. When samples were from regurgitant or stomachs, diet items were identified to lowest possible taxon. Scales were taken from fish for age determination when possible. Weights of individual fish from regurgitant and stomach samples were estimated

using length-weight regressions developed from gillnet and trawl surveys conducted on Oneida Lake (Cornell Biological Field Station, *unpublished data*). Common mudpuppy *Necturus maculosus maculosus* weights were determined using the length-weight relationship from VanDeValk and Coleman (2010). Analysis of pellets for 1997 is described in detail in VanDeValk et al. (2002). Taxa were identified based on otoliths and bones found in the pellets (Hansel et al. 1988) and age of walleye and yellow perch in diets was inferred from fish length to otolith length regressions.

Diet composition by year was determined using percent by number, percent by weight, and frequency of occurrence. These three measures give complementary information on the diet of a predator. To examine the overall importance of a diet item, we used an index of relative importance (IRI; Pinkas et al. 1971). The IRI incorporates diet item weight, number, and frequency of occurrence to reduce bias associated with presenting diet composition consisting of many small prey items or a few large prey items (Liao et al. 2001). The IRI of a prey taxon (IRI_a) was derived as:

$$IRI_a = \%F(\%N + \%W),$$

where %F is percent frequency of occurrence, %N is percent by number, and %W is percent by weight of prey item *a*. Percent IRI_a ($\%IRI_a$) was then calculated for prey taxon *a* in the sample:

$$\%IRI_a = \frac{100 * IRI_a}{\sum_{a=1}^{n} IRI_a},$$

where *n* is the number of different prey taxa in the diet (Cortez 1997). The $\%IRI_a$ values range from 0-100, with 0 indicating no dietary importance and 100 indicating that prey type was the only one consumed, and the sum of $\%IRI_a$ in a given year and season equals 100. The %IRI was used to describe prey importance in the diet because 1) the inputs only rely on diet composition data therefore results can be easily compared to cormorant diet composition in other systems (Cortez 1997; Hart et al. 2002), and 2) dietary indices which incorporate all three metrics were found to be superior to any singular index alone (Liao et al. 2001). Due to limited information (inability to calculate frequency of occurrence or prey weight in some years), not all samples were included in the %IRI comparisons: regurgitant samples from 1995-1996 and pellet samples from 1997 were omitted from %IRI calculations (see Table 2.1 for sample sizes included in %IRI calculations), however these omitted samples were included in Table 2.2.

Species selectivity was determined by year and season according to the selection ratio ($\hat{w}_i$) outlined in Manly et al. (2002):

$$\hat{w}_i = o_i/\pi_i,$$

where o_i = proportion of species *i* in diet sample and π_i = proportion of species *i* in environment. Selectivity was determined for only the five fish species for which population estimates were available. Species-specific age ranges used were based on the ages consumed by cormorants (Coleman 2009; Cornell Biological Field Station, *unpublished data*) and intentionally excluding age-0 walleye, white perch, and yellow perch to better expose consumption patterns regarding ages 1+ of these species. Comparisons by season were conducted for gizzard shad (age 0), emerald shiner (age 0 and 1), white perch (age 1-3), yellow perch (age 1-4), and walleye (age 1-3). Abundance estimates for white perch used only in the selectivity analysis were estimated using gillnet catch-curve analysis. Chi-squared

Table 2.1. Number of cormorant diet samples, collection date range, and number of dates sampled (no. dates) by year and season (summer/fall) included in relative importance calculations for each sample type from Oneida Lake, 1995-2009. Numbers in parentheses are the total number of diet items identified by season (summer/fall). No regurgitant samples from 1995 and 1996 or pellet samples from 1997 were included in %IRI calculations.

	Sample Type		Date Range		No. Dates
	Regurgitant	Stomachs	Summer	Fall	(S / F)
1995	480* (791 / 226)	1 / 47 (57 / 314)	5/7 – 7/31	8/3 - 10/31	29 / 18
1996	589* (1151 / 98)	29 / 42 (55 / 966)	4/12 – 7/22	8/3 – 10/19	20 / 15
1997		101 / 37** (897 / 256)	5/2 – 7/30	8/5 – 9/12	12 / 3
1998	46 / 4 (255 / 20)		7/2 – 7/17	8/2	4 / 1
1999	182 / 6 (883 / 18)		5/28 – 7/12	8/19	9 / 1
2000	156 / 8 (462 / 16)		5/27 – 7/27	8/2	15 / 1
2001	210 / 0 (904 / 0)	0 / 14 (0 / 148)	6/15 – 7/27	9/5 – 9/11	10 / 2
2002	243 / 0 (653 / 0)	0 / 14 (0 / 139)	5/30 – 7/17	8/21 – 8/28	10 / 2
2003	131 / 1 (337 / 10)	0 / 3 (0 / 3)	5/27 – 7/23	8/7 – 8/28	14 / 3
2004		0 / 31 (0 / 445)		9/2 – 9/29	0 / 5
2005		10 / 14 (6 / 78)	6/1	8/3 – 9/14	1 / 6
2006		6 / 36 (10 / 339)	7/24	8/24 – 12/6	1 / 8
2007		9 / 67 (16 / 381)	6/13 – 7/23	8/6 – 9/27	6 / 24
2008		30 / 131 (47 / 1942)	4/14 – 7/28	8/4 – 10/23	13 / 20
2009		64 / 72 (143 / 867)	4/19 – 7/29	8/4 – 9/23	13 / 26

*The number of regurgitant samples by season during 1995 and 1996 could not be verified. The total number of samples and individual diet items by season were known.
**All diet samples from 1997 were from pellet samples.

tests were used to assess if selection was random during each season. The log-likehood X^2 test statistic was used:

$$X_L^2 = 2\sum_{i=1}^{I} u_i \log_e\{\frac{u_i}{u_+ \pi_i}\},$$

where u_i = count of species *i* in diet and u_+ = total count of diet items in a season (Manly et al. 2002). If selection was found to be non-random within a season, further X^2 tests of significance were performed on the individual selection indices ($\hat{w}_i$) and Bonferroni-corrected simultaneous confidence intervals were constructed around the species' selection indices. Significant differences between species' $\hat{w}_i$ within a single sampling season was determined by comparing the confidence intervals around the estimate ($\hat{w}_i - \hat{w}_j$). If zero was included in the interval, then selection indices were deemed statistically similar. All tests performed used $\alpha = 0.05$ as well as Bonferroni corrections when possible to ensure conservative estimates and intervals (more details are in Manly et al. 2002).

Finally, to address the influence of changes in availability of fish species on cormorant diets and gain insights regarding the influence of fish community structure on cormorant consumption, seasonal correlations between the proportions by number found in cormorant diet samples and the density estimates in Oneida Lake were examined for the same five fish species (and age ranges) as above. We used a one-tailed Spearman's rank correlation to test for a positive relationship between prey fish density and proportion in the diet (Bonferroni adjusted $\alpha < 0.005$) and a negative relationship with increasing density of alternative prey species (Bonferroni adjusted $\alpha < 0.00125$). Multiple linear regression models were also used to complement the correlation results while controlling for effects of other species. Response variables (proportion of species in diet) and predictor variables (density of species in lake) were transformed or removed (predictors) as needed to meet model assumptions and improve model fit. A response species own density was never removed as a predictor. Single points (years) were removed from some models when model diagnostics (Cook's distance, influence

plots, and outlier test) deemed this appropriate. No more than one point was removed from any analysis. All final linear models produced satisfactory regression diagnostics and passed model assumptions. To directly evaluate evidence of prey switching by cormorants, one-tailed Spearman Rank Correlations were performed on $\hat{w}_i$ with density of species *i* (Bonferroni adjusted $\alpha < 0.005$). Prey switching would be indicated by an increase in selectivity with increased density. All correlations and multiple linear models were done using the statistical program R® v.2.1.

RESULTS

A total of 25 different prey taxa were identified in cormorant diet samples from 1995 to 2009, 23 fish species/genera, the common mudpuppy, and crayfish spp. (Table 2.2). Unidentifiable diet items constituted as much as 11.6% by number in the year when pellets were used (1997), but the overall number of unidentifiable items over the course of the study was 2% (summer total = 1.7%, fall total = 2.5%). Unidentifiable items were not further considered in the analyses. Samples (individual birds) containing >1 unidentifiable item were also excluded from IRI analyses to eliminate inflated importance which would be given to remaining diet items in the sample (e.g., increased %W value); however, identified items from these birds were included in all other tables and analyses where appropriate.

Despite consistent occurrence of some prey species in cormorant diets, there were large annual and seasonal variations in numbers of other species consumed (Table 2.2). *Lepomis* spp., walleye, and yellow perch were present in cormorant diets every sampling year (except walleye in 2006). Logperch *Percina caprodes* were present in large numbers from 1995-2004 and represented an especially large proportion in 1998. Gizzard shad were present in large numbers beginning in 2001 and every year after, especially during fall. Across all years, the most common identified species numerically in summer were yellow perch (57.0%), walleye (9.7%), and logperch (8.9%) and in fall gizzard shad (54.8%), yellow perch

Table 2.2. Cormorant diet composition by number (%) from Oneida Lake including all identifiable diet items from all collected samples, 1995-2009. Percentages are from combined regurgitant, stomach, and pellet samples. S=summer diets, F=fall diets. No summer samples were taken in summer 2004. Sample sizes and number of identified prey are in Table 2.1.

	1995		1996		1997		1998		1999		2000		2001		2002	
Diet Item	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F
Banded Killifish	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Black Crappie	0.0	0.0	0.0	0.1	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Bowfin	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brown Bullhead	0.6	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Burbot	3.1	0.2	1.5	0.2	1.1	2.0	0.4	0.0	0.1	0.0	0.4	0.0	1.2	0.0	1.4	0.0
Channel Catfish	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clupeid spp.	0.2	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Common Mudpuppy	0.0	0.0	0.0	0.0	0.2	0.0	0.4	0.0	0.0	0.0	1.7	0.0	0.8	0.0	0.9	0.0
Crayfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Emerald Shiner	0.0	25.4	0.2	38.0	11.4	9.0	3.6	65.0	14.7	0.0	3.9	0.0	2.1	4.1	13.0	7.9
Esox spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.4	0.0	0.0	0.0	0.3	0.0
Fallfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Freshwater Drum	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gizzard Shad	7.3	8.9	0.2	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	75.7	6.4	80.6
Lepomis spp.	3.5	1.7	6.1	1.5	9.1	11.3	4.9	5.0	10.3	16.7	13.2	18.8	2.2	0.7	3.4	0.0
Largemouth Bass	0.2	0.4	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Logperch	22.6	17.0	0.4	5.2	0.2	0.0	51.6	15.0	2.9	0.0	0.9	6.3	12.3	0.7	2.5	0.0
Rock Bass	2.0	0.0	0.8	0.8	1.8	3.9	1.3	0.0	1.0	5.6	3.2	0.0	0.8	0.0	1.7	0.0
Smallmouth Bass	2.0	3.0	1.3	0.7	0.7	2.3	0.9	0.0	0.6	0.0	3.7	0.0	0.3	0.7	1.2	0.0
Tessellated Darter	0.5	1.5	0.8	1.4	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.0	0.0
Troutperch	5.3	0.2	0.0	0.0	2.1	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0
Walleye	13.2	5.9	5.0	2.2	2.6	1.2	4.0	5.0	3.5	5.6	10.2	43.8	15.5	1.4	14.4	6.5
White Perch	0.2	6.3	0.1	0.1	0.6	4.7	0.4	0.0	0.5	0.0	1.9	0.0	1.1	0.7	4.3	0.0
White Sucker	1.7	0.0	0.5	0.1	0.7	1.2	0.4	0.0	0.1	0.0	0.4	6.3	0.2	0.0	0.6	0.0
Yellow Perch	37.3	28.7	83.1	49.4	68.9	62.1	31.6	10.0	65.8	72.2	59.3	25.0	63.3	16.2	45.8	5.0

	2003		2004	2005		2006		2007		2008		2009		Grand Total	
Diet Item	S	F	F	S	F	S	F	S	F	S	F	S	F	S	F
Banded Killifish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Black Crappie	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Bowfin	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brown Bullhead	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Burbot	1.5	7.7	0.0	16.7	0.0	10.0	0.0	6.3	0.5	2.1	0.1	0.0	0.1	1.7	0.3
Channel Catfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clupeid spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Common Mudpuppy	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Crayfish	0.0	0.0	0.2	33.3	2.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1
Emerald Shiner	12.2	0.0	19.8	0.0	25.6	10.0	0.6	0.0	11.3	0.0	6.5	0.7	4.6	5.5	14.2
Esox spp.	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.4	0.1	0.0	0.0	0.2	0.0
Fallfish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Freshwater Drum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.1
Gizzard Shad	0.3	76.9	63.6	0.0	15.4	20.0	92.6	6.3	65.6	51.1	86.8	2.1	75.9	3.5	54.8
Lepomis spp.	5.6	0.0	0.4	0.0	2.6	0.0	0.6	0.0	2.4	6.4	0.4	14.7	1.7	6.4	1.9
Largemouth Bass	0.3	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.1
Logperch	8.9	0.0	12.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	8.9	3.5
Rock Bass	2.4	0.0	0.2	0.0	0.0	40.0	0.0	18.8	0.8	2.1	0.1	10.5	1.0	1.7	0.5
Smallmouth Bass	1.8	0.0	0.4	0.0	12.8	0.0	0.3	0.0	2.1	0.0	0.2	0.0	0.1	1.2	0.9
Tessellated Darter	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.4
Troutperch	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	1.2	0.1
Walleye	18.1	7.7	1.1	50.0	10.3	0.0	0.0	0.0	2.9	4.3	0.3	2.8	0.8	9.7	2.0
White Perch	3.6	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0	12.8	0.2	5.6	0.3	1.2	0.8
White Sucker	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1
Yellow Perch	43.0	7.7	1.6	0.0	29.5	20.0	5.9	56.3	14.4	14.9	5.3	60.1	15.2	57.0	20.1

Note: *Esox* spp. includes chain pickerel (*Esox niger*), northern pike (*E. lucius*), and *Esox* spp.; *Lepomis* spp. include bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*); White perch include white perch (*Morone americana*) and any white bass (*M. chrysops*) which were found.

(20.1%), and emerald shiner (14.2%) were the most frequently consumed species. When age-0 gizzard shad were present, they typically began to occur in cormorant diet samples in late July or early August at sizes larger than 45 mm and continued to be present in the samples throughout the fall season.

The ten species with the highest overall percent by weight were (in order) yellow perch, walleye, gizzard shad, *Lepomis* spp., burbot *Lota lota*, white perch, white sucker *Catostomus commersonii*, rock bass *Ambloplites rupestris*, smallmouth bass, and logperch (Table 2.3). Similar to percent by number, percent by weight was highly variable across years and seasons. Notable weight contributions by species other than the ten listed above include emerald shiner in fall 1996 (4.2%) and fall 1998 (21.8%); brown bullhead *Ameiurus nebulosus* in summer 1995 (6.5%); and *Esox* spp. during the summer and fall of 2008 (5.3% and 4.0%).

The six species with the highest overall percent by number (emerald shiner, gizzard shad, *Lepomis* spp., logperch, walleye, and yellow perch) were assessed in more detail using %IRI. Yellow perch occurred in cormorant diets consistently in both summer and fall and had high dietary importance during the summer season (%IRI range of 16.5-84.2 out of a maximum of 100, excluding 2005 when %IRI=0; Figure 2.1a). Gizzard shad had the highest %IRI values of any prey taxa during the fall from 2001-2009 (average 71.0; Figure 2.1b) but not from 1995-2000 (average 0.1). Yellow perch had high %IRI in the fall only in years when consumption of gizzard shad was low (gizzard shad %IRI < 5, years 1995-2000 and 2005, average yellow perch 47.0). Walleye had variable dietary importance during the summer (%IRI range 0-63.2, average 15.1) and fall (%IRI range 0-62.0, average 15.5). Emerald shiner %IRI ranged from 0-3 (average 0.6) in the summer and 0-36.1 (average 5.0) in the fall. *Lepomis* spp. %IRI ranged from 0-11.8 (average 3.1) in the summer and 0-18.3 (average 2.8) in the fall. Logperch %IRI ranged from 0-22.2 (average 2.0) in the summer and 0-12.9 (average 1.5) in the fall. Cormorant diets in the summer showed greater variability, as

Table 2.3. Cormorant diet composition by weight (%) for the ten species comprising largest overall diet weight from Oneida Lake including all identifiable diet items from all collected samples, 1995-2009. Percentages are from combined regurgitant and stomach samples when weight estimates were available (not available in 1997). S=summer diets, F=fall diets. No summer samples were taken in summer 2004. Sample sizes and number of identified prey are in Table 2.1. BUT = burbot; GIS = gizzard shad; *Lepomis* = *Lepomis* spp.; LOP = logperch; ROB = rock bass; SMB = smallmouth bass; WAE = walleye; WHP = white perch; WHS = white sucker; YEP = yellow perch.

		Species									
Year		BUT	GIS	*Lepomis*	LOP	ROB	SMB	WAE	WHP	WHS	YEP
1995	S	9.7	1.8	3.3	2.9	2.3	1.3	25.6	0.2	3.6	41.7
	F	0.4	2.6	2.3	4.2	0.0	4.7	36.5	8.5	0.0	35.5
1996	S	6.8	0.1	5.6	0.0	2.1	4.2	19.3	0.6	2.8	57.8
	F	2.0	0.0	2.6	1.6	2.6	0.8	39.0	0.2	0.2	44.8
1998	S	1.5	0.0	8.3	7.6	2.1	2.2	19.5	2.3	9.8	44.5
	F	0.0	0.0	6.7	16.1	0.0	0.0	25.2	0.0	0.0	30.2
1999	S	0.4	0.0	16.2	0.6	0.8	2.8	26.0	1.5	2.6	44.3
	F	0.0	0.0	10.9	0.0	22.1	0.0	11.4	0.0	0.0	55.6
2000	S	0.9	0.0	6.7	0.1	1.4	4.6	29.2	3.7	4.9	45.0
	F	0.0	0.0	14.9	0.1	0.0	0.0	41.9	0.0	40.1	3.0
2001	S	5.0	0.0	5.0	1.4	0.6	2.0	34.4	4.9	3.9	40.8
	F	0.0	71.5	0.1	0.2	0.0	0.3	1.6	0.2	0.0	25.6
2002	S	1.0	2.7	4.3	0.2	1.9	3.3	33.7	6.1	6.9	37.3
	F	0.0	29.0	0.0	0.0	0.0	0.0	40.2	0.0	0.0	30.5
2003	S	4.5	0.7	4.2	0.6	3.4	1.2	50.1	6.9	4.5	20.4
	F	12.3	3.8	0.0	0.0	0.0	0.0	62.8	0.0	0.0	21.1
2004	F	0.0	73.1	5.5	5.4	1.8	0.3	4.0	0.0	0.0	5.3
2005	S	62.3	0.0	0.0	0.0	0.0	0.0	35.6	0.0	0.0	0.0
	F	0.0	3.8	1.4	0.0	0.0	4.8	63.2	0.0	0.0	24.9
2006	S	17.0	50.5	0.0	0.0	13.2	0.0	0.0	0.0	0.0	19.1
	F	0.0	89.1	2.5	0.0	0.0	0.1	0.0	0.0	0.0	8.2
2007	S	13.3	0.0	0.0	0.0	8.0	0.0	0.0	22.4	0.0	56.3
	F	8.7	48.1	3.9	0.0	1.4	0.3	21.5	0.0	0.0	15.1
2008	S	5.0	22.3	5.3	0.0	3.2	0.0	23.8	26.3	0.0	8.8
	F	2.8	58.7	2.0	0.0	1.4	0.1	5.6	0.1	0.0	24.3
2009	S	0.0	12.1	13.2	0.1	9.4	0.0	6.9	14.6	0.0	43.6
	F	1.9	32.4	13.5	0.0	14.1	0.0	16.2	1.4	0.0	19.7
Overall %		3.9	9.2	5.6	1.0	2.3	2.3	27.2	3.6	3.5	38.2

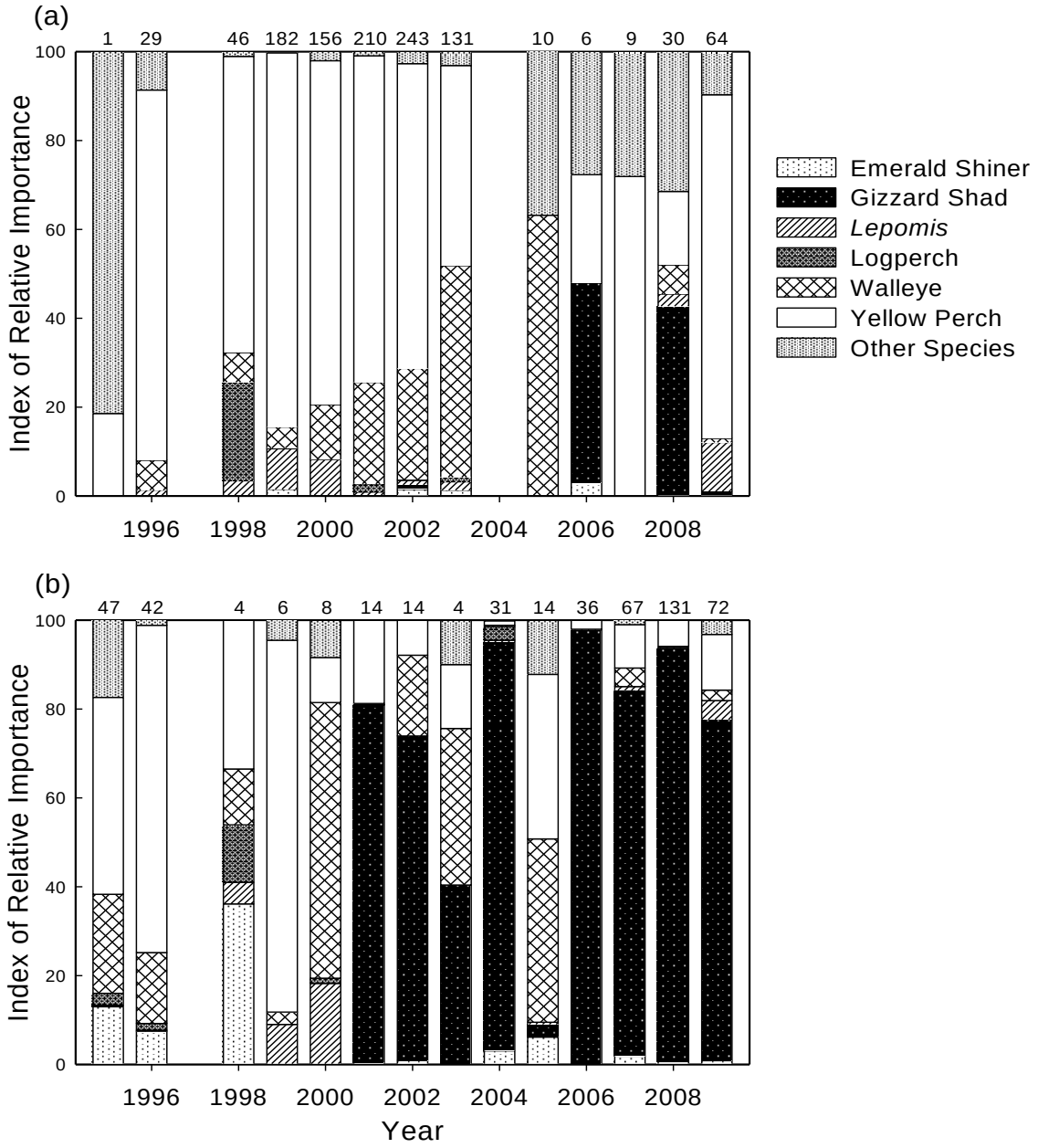


Figure 2.1. Index of relative importance (%IRI) by year and season (a = summer, b = fall) for cormorant diets on Oneida Lake for the most frequently consumed items, 1995-2009. The numbers on the top of the bars are the number of diet samples for the given year and season. 'Other' included all other species' relative importance values combined (see Table 2.2 for list of species found in a particular year).

indicated by the dietary importance of the 'other' category (%IRI range 0.3-81.4, average 18.0; see Table 2.2 for all 'other' fish species found in diet samples).

Assessments of relationships between fish density estimates and cormorant consumption (percent by number) for five species (emerald shiner, gizzard shad, walleye, white perch, and yellow perch) revealed four significant Spearman's rank correlations at the $\alpha = 0.05$ level and only one significant Spearman's rank correlation at the Bonferroni adjusted alpha level (Figure 2.2). Only emerald shiner consumption was significantly correlated with emerald shiner density ($\rho = 0.69$, $P = 0.003$) during summer at the Bonferroni adjusted alpha ($\alpha < 0.005$). Correlations significant at the $\alpha = 0.05$ level were consumption of gizzard shad positively correlated with gizzard shad density in fall ($\rho = 0.63$, $P = 0.006$); white perch consumption negatively correlated with walleye density in fall ($\rho = -0.50$, $P = 0.03$); and consumption of yellow perch negatively correlated with gizzard shad density ($\rho = -0.61$, $P = 0.008$) in fall.

The multiple linear regressions resulted in four models which were significant ($P < 0.05$). Cormorant consumption of emerald shiners in summer increased with emerald shiner and white perch density and decreased with increased yellow perch density (Table 2.4). White perch consumption in summer displayed positive relationships with gizzard shad and yellow perch densities. Gizzard shad consumption in fall increased with gizzard shad density. Yellow perch consumption in fall had negative relationships with gizzard shad and white perch densities and a positive relationship with emerald shiner density.

Cormorants did not select prey taxa at random in any year-season combination investigated (Table 2.5, Appendix I). Tested selection indices ($\hat{w}_i$) among individually consumed species produced variable results (Table 2.5). Of the 145 individual $\hat{w}_i$, 36 could not be confidently evaluated due to cormorants not consuming any of that taxon in a specific year and season; 75 individual $\hat{w}_i$ were found to be significant ($X^2 > \pm 2.33$) and 34 $\hat{w}_i$ found

Figure 2.2. Spearman's rank correlations of fish species abundance to proportion by number for cormorant diets collected during summer (open diamonds (◊) with solid lines) and fall (filled circles (●) with dashed lines) on Oneida Lake. One-tailed correlations significant at $\alpha < 0.05$ are identified and correlations significant at the Bonferroni adjusted level are further indicated (*).

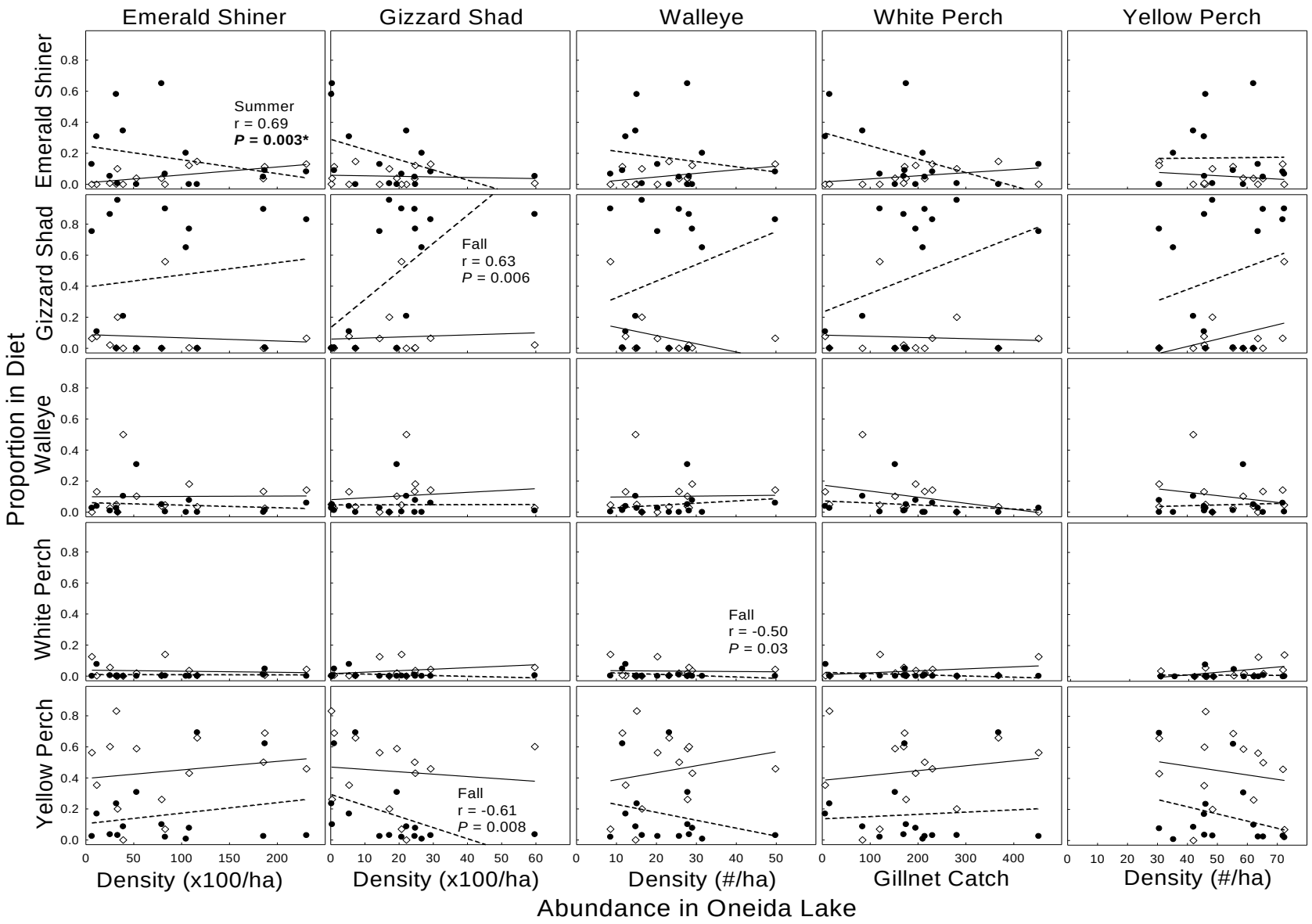

Emerald Shiner
Gizzard Shad
Walleye
White Perch
Yellow Perch
Proportion in Diet
Summer
r = 0.69
P = 0.003*
Fall
r = 0.63
P = 0.006
Fall
r = -0.50
P = 0.03
Fall
r = -0.61
P = 0.008
Density (x100/ha)
Density (x100/ha)
Density (#/ha)
Gillnet Catch
Density (#/ha)
Abundance in Oneida Lake

Table 2.4. Multiple linear regression results comparing proportion of a species in the diet to density of all species. If predictor was found to be significant (*), the direction of the corresponding coefficient was included in parenthesis. Models found to be significant ($P < 0.05$) are bolded. Note: EMS = emerald shiner; GIS = gizzard shad; WAE = walleye; WHP = white perch; YEP = yellow perch.

			Overall Model	
Season	Response (Proportion in Diet)	Included Predictors (Species Density)	Adj. R^2	*P*
Summer	Emerald Shiner	**EMS*(+), WHP*(+), YEP*(-)**	**0.708**	**0.001**
	Gizzard Shad	GIS, EMS, WAE, WHP, YEP	-0.441	0.92
	Walleye	WAE, EMS, WHP, YEP	0.298	0.15
	White Perch	**WHP, GIS*(+), WAE, YEP*(+)**	**0.724**	**0.011**
	Yellow Perch	YEP, EMS, GIS, WAE, WHP	0.394	0.92
Fall	Emerald Shiner	EMS, GIS, WHP, YEP	0.091	0.32
	Gizzard Shad	**GIS*(+), WAE, WHP, YEP**	**0.473**	**0.048**
	Walleye	WAE, EMS, GIS, WHP, YEP	-0.228	0.75
	White Perch	WHP, EMS, WAE, WHP	0.32	0.096
	Yellow Perch	**YEP, EMS*(+), GIS*(-), WAE, WHP*(-)**	**0.677**	**0.02**

Table 2.5. Summary of significance tests of individual $\hat{w}_i$ (species selectivity) calculated based on the occurrence of five prey species in double-crested cormorant diets from Oneida Lake, NY, 1995-2009, according to season (S = summer, F = fall). Full details of these tests and individual comparisons are found in Appendix A. Significant negative selection is indicated if $\hat{w}_i < 1$. Significant positive selection is indicated if $\hat{w}_i > 1$.

	Time	Significant (+)		Significant (-)		Non-Significant	
Species	Period	S	F	S	F	S	F
Emerald Shiner	1995-2000	0	0	5	3	0	2
	2001-2009	0	0	4	7	1	0
Gizzard Shad	1995-2000	0	0	3	1	0	2
	2001-2009	1	8	4	0	1	0
Walleye	1995-2000	6	3	0	0	0	2
	2001-2009	3	2	0	0	2	5
White Perch	1995-2000	1	2	0	0	5	1
	2001-2009	5	0	0	0	1	2
Yellow Perch	1995-2000	6	4	0	0	0	1
	2001-2009	5	2	0	0	2	7

to be non-significant. In instances where $u_i < 5$, significance tests should be interpreted with caution (Manly et al. 2002). Comparisons of $\hat{w}_i$ between taxa within a season produced variable results which are detailed in Appendix I. Between-taxa comparisons with a taxon containing $u_i < 5$ in a single season were not produced in order to provide only conservative comparisons from which to draw conclusions (Manly et al. 2002). Finally, correlations between prey density and $\hat{w}_i$ to investigate potential prey switching behavior by cormorants revealed two correlations at the $\alpha = 0.05$ level and only one significant Spearman's rank correlation at the Bonferroni adjusted alpha level ($\alpha = 0.005$); gizzard shad in the fall ($\rho = 0.71$, $P = 0.001$) and emerald shiner in the summer ($\rho = 0.55$, $P = 0.02$).

DISCUSSION

Establishing the prey preferences of a top predator furthers understanding of predator-prey interactions and the influence of alternative prey on predator impacts. Cormorants are top predators in aquatic systems and determining factors which influence their prey selection provides insight to the potential predation effects on recreational and commercial fisheries in areas where cormorants reside. As observed in other systems (Neuman et al. 1997; Diana et al. 2006; Seefelt and Gillingham 2006; Johnson et al. 2010; DeBruyne et al. 2012; Coleman et al. in press), cormorant diets on Oneida Lake consisted of a variety of fish species and other prey items (crayfish, mudpuppy) and included representatives of most available prey groups. Yellow perch, walleye, emerald shiner, *Lepomis* spp. and logperch were consumed throughout the year, but gizzard shad were mainly consumed in the fall season, and consumption corresponded to years of large age-0 cohorts. Although cormorants feed on a variety of prey, our study demonstrates that they are selective predators, particularly selecting for emerald shiner and age-0 gizzard shad when available and larger than 45 mm. Decreased fall consumption and selection of yellow perch was associated with high age-0 gizzard shad

density. The importance of a seasonally available prey group on use of other species has important implications for assessing impacts of cormorants on prey species.

Cormorant consumption and $\hat{w}_i$ for emerald shiners and gizzard shad increased as these species became more abundant, but similar increases in consumption with increased availability were not observed with other common species in cormorant diets, such as walleye and yellow perch. These results suggest that cormorants display prey switching (Murdoch 1969) to emerald shiners and gizzard shad when available in high abundance. Age-0 gizzard shad and emerald shiners lack spines, are soft-bodied, and typically form schools, whereas adult percids do not traditionally form large schools, so the pursuit and handling time for walleye and yellow perch could possibly be higher per individual prey than for gizzard shad and emerald shiner. Cormorants are also known to utilize social foraging strategies considered to be more efficient for pursuing schooling prey (Bartholomew 1942), and large flocks of foraging cormorants were routinely observed on Oneida Lake annually starting around the first week of August (Coleman 2009). Six of the eight years with the highest yellow perch densities in Oneida Lake had the lowest fall yellow perch consumption by cormorants, presumably because of the high age-0 gizzard shad abundance. In 2008, gizzard shad had high relative importance during the summer, corresponding to rapid growth of age-0 gizzard shad in Oneida Lake (Cornell Biological Field Station, *unpublished data*), making them vulnerable to cormorant predation in late July. When gizzard shad are consumed during the summer season, it further reduces the predation pressure on yellow perch and walleye, indicated by their lower %IRI and $\hat{w}$ during summer 2006 (walleye) and 2008 (walleye and yellow perch) by cormorants. Overall, these results contradict the widely held perception of cormorants as non-selective predators, instead indicating that cormorants prefer gizzard shad and emerald shiner over walleye and yellow perch in Oneida Lake and that these soft-bodied prey species will buffer predation on walleye and yellow perch from cormorants when abundant.

Further evidence for prey switching behavior by cormorants is evident in the prey selection analysis. We demonstrate a significant relationship of increased cormorant selection with increased gizzard shad densities. Concurrently, selection for yellow perch and walleye was absent in most years post-2001 during the fall, even though densities of percids were high. Positive selection for walleye was restricted to pre-2006 with no positive selection during the fall since 2002 (except 2005). Yellow perch were selected for during both summer and fall seasons from 1995-2000, but only in the summer from 2001-2007. The avoidance of emerald shiners and age-0 gizzard shad during the summer months is not surprising since these prey species are not consumed by cormorants until the fall (due to fish size of age-0). Unless summer growth was good in a particular year, age-0 gizzard shad and emerald shiners were not heavily utilized by cormorants and the selection results confirm the seasonality of these food resources for the cormorants. All positive selection on gizzard shad occurred post-2001 during the fall (except summer 2008 when gizzard shad growth was rapid), when we have consistently large age-0 gizzard shad densities. Cormorants positively selected percids during summer and fall when large age-0 gizzard shad cohorts were not available; however, in years with high age-0 gizzard shad densities, cormorants no longer displayed selection for percids and instead displayed positive selection for gizzard shad.

The IRI of gizzard shad was high from 2001-2009 during the fall season. No other single fish species displayed this type of dominance in cormorant diets, even when a particular species was at high densities in Oneida Lake. The dominance of gizzard shad in the fall, even with high densities of yellow perch and white perch, further supports that cormorants select for gizzard shad in the fall on Oneida Lake. Similar dominance of soft-bodied fishes in cormorant diets is found in eastern Lake Ontario and the Niagara River, where diets are dominated by round goby (Johnson et al. 2010; Coleman et al. 2012) and eastern Lake Ontario, northern Lake Michigan, and Lake Champlain where alewife *Alosa psuedoharengus* can dominate the diet (Johnson et al. 2002; Seefelt and Gillingham 2006;

DeBruyne et al. 2012). Thus, cormorants may be selective towards soft-bodied fish in other areas as well.

Cormorant diets in Oneida Lake displayed an additional characteristic which suggests cormorants are selective predators. White perch has become a major component of the Oneida Lake fish community; some years outnumbering yellow perch in gillnet surveys (Rudstam and Jackson 2012). Yet white perch were not consumed by cormorants at a rate consistent with their availability. This suggests cormorants were avoiding white perch when foraging. Reasons for avoiding specific fish species are not known; however it could be related to fish body shape, the presence of spines, or a defense behavior exhibited by white perch. However, *Morone* spp. do comprise larger proportions of cormorant diets in other systems (Neuman et al. 1997; Fenech et al. 2004; Dalton et al. 2009; DeBruyne et al. 2012), indicating there is not a physical constraint (such as gape limitation) preventing increased white perch consumption in Oneida Lake. Other factors, such as habitat selection by white perch and availability of more preferred prey may be responsible for the low utilization of white perch by cormorants in Oneida Lake.

Even though cormorants forage throughout Oneida Lake (Coleman et al. 2005), they may not be foraging in all locations during the fall sampling period (Aug-Oct) when the macrophyte coverage in Oneida Lake increases, potentially covering up to 53% of the lake bottom (Zhu et al. 2006). This increase in habitat complexity may deter cormorants from foraging in shallower waters, protecting prey fish in these refuge areas, such as yellow perch, from cormorant predation (Carpentier et al. 2009; Eisenhower and Parrish 2009). Both increased habitat complexity and increased shad schools in the pelagic zone could be reducing predation on desired sportfish species (compared to mid-1990s) without any external management actions.

Rudstam et al. (2004) concluded that cormorants contributed significantly to the observed declines of walleye and yellow perch populations in the 1990s in Oneida Lake (see

also Irwin et al. 2008). This was based on diet data from 1995-2001, years with low gizzard shad abundance in Oneida Lake. Since then, gizzard shad abundance has increased, likely as a result of shorter winters (Fetzer et al. 2011), cormorant consumption of gizzard shad has increased, and cormorant consumption of walleye and yellow perch has decreased. Extrapolation of diet information in Rudstam et al. (2004) over-estimates the effect of cormorants on walleye and yellow perch in years when gizzard shad are abundant. Over-estimating predation effects on walleye and yellow perch is more likely for the fall season than the summer season since cormorants do not typically consume age-0 gizzard shad until late July-August. Cormorants on islands in eastern Lake Ontario displayed similar shifts in diet with the establishment of a new forage fish, the round goby (Johnson et al 2009, 2010). Initial studies revealed significant negative effects on smallmouth bass and yellow perch populations (Lantry et al. 2002; Burnett et al. 2002), but by 2005 round goby was the dominant diet item (Johnson et al. 2006, 2010). On Oneida Lake, intense predation pressure can occur during fall migration, when the daily number of cormorant adults on the lake could exceed 2000 individuals (Coleman 2009). If there are consistent, large year classes of gizzard shad produced, the impact of cormorants on walleye and yellow perch populations during fall would be buffered by cormorants feeding on gizzard shad. Thus, the predation pressure on percids may be greatest during spring and summer when large refuge areas have not yet developed and age-0 gizzard shad are not large enough to be selected by cormorants. We suggest that the abundance of preferred alternative prey is a significant factor determining potential for cormorants to have detrimental impacts on recreationally and commercially important fish species. Results from this study emphasize the importance of long-term monitoring and targeted studies of predators and prey in aquatic systems, especially those undergoing marked ecological change.

ACKNOWLEDEMENTS

Funding and support for this project was provided by New York State Department of Environmental Conservation (New York Federal Aid in Sport Fish Restoration Program); USDA-APHIS Wildlife Services; New York Cooperative Fish and Wildlife Research Unit, USGS; Oneida Lake Fish Cultural Station; The Jack H. Berryman Institute; and by a grant from the USFWS, Sport Fish Restoration. We thank the following individuals for their invaluable contributions to this effort: John Forney, Connie Adams, Milo Richmond, Tom Brooking, Scott Krueger, Ken Preusser, Justin Gansowski, Martin Lowney, Travis DeVault, Rich Chipman, Carl Cranker, Elizabeth Cranker, Bridger and Kelly Thompson, and the host of students and researchers who have contributed to long-term fish and waterbird monitoring efforts at CBFS. We also thank Milo Richmond, Richard Beamish, and three anonymous reviewers for their comments which improved the manuscript. Mention of trade names or commercial products in this manuscript does not imply endorsement or recommendation for use by the U.S. Government. This is contribution number 290 from the Cornell Biological Field Station and is also a product of the New York Cooperative Fish and Wildlife Research Unit.

LITERATURE CITED

Bartholomew, G. A. 1942. The fishing activities of double-crested cormorants on San Francisco Bay. Condor 44:13-21.

Burnett, J. A. D., N. H. Ringler, B. F. Lantry, and J. H. Johnson. 2002. Impact of double-crested cormorant (*Phalacrocorax auritus*) piscivory on the yellow perch (*Perca flavescens*) populations in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28:202-211.

Carpentier, A., L. Marion, J.-M. Paillisson, A. Acou, and E. Feunteun. 2009. Effects of commercial fishing and predation by cormorants on the *Anguilla anguilla* stock of a shallow eutrophic lake. Journal of Fish Biology 74:2132-2138.

Claypoole, K. 1988. First nesting of the double-crested cormorant at Oneida Lake, New York. The Kingbird 38:235-236.

Connelly, N. A. and T. L. Brown. 1991. Net economic value of the freshwater recreational fisheries of New York. Transactions of the American Fisheries Society 120:770–775.

Coleman, J. T. H. 2009. Diving behavior, predator-prey dynamics, and management efficacy of double-crested cormorants in New York State. Ph.D Dissertation. Cornell University, Ithaca, New York.

Coleman, J. T. H., C. M. Adams, M. Kandel, and M. E. Richmond. 2012. Eating the invaders: The prevalence of the invasive round goby (*Apollonia melanostomus*) in the diet of double-crested cormorants on the Niagara River. Waterbirds 35 (Sp1): 103-113.

Coleman, J. T. H., M. E. Richmond, L. G. Rudstam, and P. M. Mattison. 2005. Foraging location and site fidelity of the double-crested cormorant on Oneida Lake, New York. Waterbirds 28:498-510.

Cortez, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54:726-738.

Craven, S. R. and E. Lev. 1987. Double-crested cormorants in the Apostle Islands, Wisconsin, USA: population trends, food habits, and fishery depredations. Colonial Waterbirds 10:64-71.

Dalton, C. M., D. Ellis, and D. M. Post. 2009. The impact of double-crested cormorant (*Phalacrocorax auritus*) predation on anadromous alewife (*Alosa pseudoharengus*) in south-central Connecticut, USA. Canadian Journal of Fisheries and Aquatic Sciences 66:177-186.

DeBruyne R. L., T. L. DeVault, A. E. Duerr, D. E. Capen, F. E. Pogmore, J. R. Jackson, and L. G. Rudstam. Spatial and temporal comparisons of double-crested cormorant diets following the establishment of alewife in Lake Champlain, USA. Journal of Great Lakes Research 38:123-130.

DeVault, T. L., R. B. Chipman, S. C. Barras, J. D. Taylor, C. P. Cranker III, E. M. Cranker, and J. F. Farquhar. 2012. Reducing impacts of double-crested cormorants to natural resources in central New York: a review of a collaborative research, management, and monitoring program. Waterbirds 35 (Sp 1): 50-55.

Diana, J. S., S. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306-320.

Eisenhower, M. D. and D. L. Parrish. 2009. Double-crested cormorant and fish interactions in a shallow basin of Lake Champlain. Waterbirds 32:388-399.

Fenech, A. S., S. E. Lochmann, and A. A. Radomski. 2004. Seasonal diets of male and female double-crested cormorants from an oxbow lake in Arkansas, USA. Waterbirds 27:170-176.

Fetzer, W. W., T. E. Brooking, J. R. Jackson, and L. G. Rudstam. 2011. Overwinter mortality of gizzard shad: Evaluation of starvation and cold temperature stress. Transactions of the American Fisheries Society 140:1460-1471.

Fielder, D. G. 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of double-crested cormorants. Journal of Great Lakes Research 34:506-523.

Hansel, H. C., S. D. Duke, P. T. Lofty, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the American Fisheries Society 117:55-62.

Hansson, S., O. Hjerne, C. Harvey, J. F. Kitchell, S. P. Cox, and T. E. Essington. 2007. Managing Baltic Sea fisheries under contrasting production and predation regimes: ecosystem model analyses. Ambio 36:265-271.

Hart, R. K., M. C. Calver, and C. R. Dickman. 2002. The index of relative importance: an alternative approach to reducing bias in descriptive studies of animal diets. Wildlife Research 29:415-421.

Harvey, C. J., S. P. Cox, T. E. Essington, S. Hansson, and J. F. Kitchell. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. ICES Journal of Marine Science 60:939-950.

Idrisi, N., E. L. Mills, L. G. Rudstam, and D. J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on pelagic lower trophic levels of Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 58:1430-1441.

Irwin, B. J., T. J. Treska, L. G. Rudstam, P. J. Sullivan, J. R. Jackson, A. J. VanDeValk, and J. L. Forney. 2008. Estimating walleye (*Sander vitreus*) density, gear catchability, and mortality using three fishery-independent data sets for Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 65:1366-1376.

Jackson, J. R., L. G. Rudstam, S. D. Krueger, T. E. Brooking, J. L. Forney, K. T. Holeck, C. Hotaling, R. L. DeBruyne, and W. W. Fetzer. 2010. The fisheries and limnology of Oneida Lake 2000-2009. Report. New York State Department of Environmental Conservation, Albany, New York, USA.

Johnson, J. H., R. M. Ross, and R. D. McCullough. 2002. Little Galloo Island, Lake Ontario: A review of nine years of double-crested cormorant diet and fish consumption information. Journal of Great Lakes Research 28:182-192.

Johnson, J. H., R. M. Ross, R. D. McCullough, and B. Boyer. 2006. Diet composition and fish consumption of double-crested cormorants from the Little Galloo Island colony of eastern Lake Ontario in 2005. Section 14 *in* NYSDEC Annual Report 2005, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.

Johnson, J. H., R. D. McCullough, and J. F. Farquhar. 2009. Double-crested cormorant studies at Little Galloo Island, Lake Ontario in 2008: Diet composition, fish consumption and the efficacy of management activities in reducing fish predation. Section 14 *in* NYSDEC Annual Report 2008, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.

Johnson, J. H., R. M. Ross, R. D. McCullough, and A. Mathers. 2010. Diet shift of double-crested cormorants in eastern Lake Ontario associated with the expansion of the invasive round goby. Journal of Great Lakes Research 36:242-247.

Lantry, B. F., T. H. Eckert, C. P. Schneider, and J. R. Chrisman. 2002. The relationship between the abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28:193-201.

Lewis, H. F. 1929. The natural history of the double-crested cormorant (*Phalacrocorax auritus auritus* (Lesson)). Ru-Mi-Lou Books, Ottawa.

Liao, H. S., C. L. Peirce, and J. G. Larscheid. 2001. Empirical assessment of indices of prey importance in the diets of predacious fish. Transactions of the American Fisheries Society 130:583-591.

Ludwig, J. P., C. N. Hill, M. E. Ludwig, and H. J. Auman. 1989. Food habits and feeding

ecology of nesting double-crested cormorants in the upper Great Lakes, 1986-1989. Jack-Pine Warbler 67:115-126.

Manly B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies. 2nd edition. Kluwer Academic, Dordrect, The Netherlands.

Mills, E. L., J. L. Forney, M. D. Clady, and W. R. Schaffner. 1978. Oneida Lake. Pages 367-451 *in* J. A. Bloomfield, editor. Lakes of New York State Vol. II. Academic Press, Inc., New York.

Mills, E. L., J. L. Forney, K. T. Holeck. Oneida Lake: A century of biotic introductions and ecosystem change. *In* L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: Long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. in press.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335-354.

Neuman, J., D. L. Pearl, P. J. Ewins, R. Black, D. V. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54:1569–1584.

Oaten, A. and W. W. Murdoch. 1975. Switching, functional response, and stability in predator-prey systems. The American Naturalist 109:299-318.

Parker-Stetter, S. L., L. G. Rudstam, P. J. Sullivan, and D. M. Warner. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fisheries Commission Special Publication 2009-01, Ann Arbor, Michigan.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Department of Fish and Game Fish Bulletin 152:1–105.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. The American Naturalist 138:123-155.

Rudstam, L. G. and J. R. Jackson. 2011. Gill net survey of fishes of Oneida Lake, New York, 1957 - 2010. Knowledge Network for Biocomplexity. Available: http://knb.ecoinformatics.org/knb/metacat/kgordon.14.85/default. (March 2011)

Rudstam, L. G. and J. R. Jackson. 2012. Walleye abundance and length at age in Oneida Lake, NY (1957-2011). Knowledge Network for Biocomplexity. Available: http://knb.ecoinformatics.org/knb/metacat/datastar.14.49/knb. (October 2012)

Rudstam, L. G., A. J. VanDeValk, C. M. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149-163.

Rudstam, L. G., T. E. Brooking, S. D. Krueger, J. R. Jackson, and L. Wetherbee. 2011. Analysis of compensatory responses in land-locked alewives to walleye predation: a tale of two lakes. Transactions of the American Fisheries Society 140:1587-1603.

Scheaffer, R. L., W. Medenhall, and L. Ott. 2006. Elementary survey sampling 6th edition. Thomson Brooks/Cole, Belmont, California.

Seefelt, N. E. and J. C. Gillingham. 2006. A comparison of three methods to investigate the diet of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, northern Lake Michigan. Hydrobiologia 567:57-67.

Steinmetz, J., S. L. Kohler, and D. A. Soluk. 2003. Birds are overlooked top predators in aquatic food webs. Ecology 84:1324-1328.

VanDeValk, A. J., C. M. Adams, L. G. Rudstam, J. L. Forney, T. E. Brooking, M. A. Gerken, B. P. Young, and J. T. Hooper. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 131:27–39.

VanDeValk, A. J. and J. T. H. Coleman. 2010. A proposed weight-length relationship for the common mudpuppy. Herpetological Review 41:29-31.

VanDeValk, A. J., L. G. Rudstam, J. R. Jackson, and S. D. Krueger. The Oneida Lake fishery: Interactions between fishing and fish. *In* L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: Long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. in press.

Wilbur, H. M. and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. The American Naturalist 135:176-204.

Wooten, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45-64.

Zhu, B., D. G. Fitzgerald, C. M. Mayer, L. G. Rudstam, and E. L. Mills. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. Ecosystems 9:1017-1028.

APPENDIX I

Appendix I. Estimation of selection indices ($\hat{w}_i$), Manly's standardized index (B_i), Bonferroni simultaneous confidence limits, and individual selection index comparisons ($\hat{w}_i$ comps; different letter = significant difference) for the occurrence of five species in double-crested cormorant diets from Oneida Lake, NY, 1995-2009, according to season (S = summer, F = fall). Results of significance tests of $\hat{w}_i$ are designated significant by (*); (^{NA}) indicates no significance test was performed due to the prey taxa being absent from the diet ($u_i = 0$) or only one taxon consumed. Significant negative selection is indicated if $\hat{w}_i < 1$. Significant positive selection is indicated if $\hat{w}_i > 1$. Individual $\hat{w}_i$ comparisons were not performed involving species with $u_i < 5$. Note: π_i = population proportions; u_i = sample count; $u+\pi_i$ = expected count; o_i = used sample proportion. EMS = emerald shiner; GIS = gizzard shad; WAE = walleye; WHP = white perch; YEP = yellow perch.

								Bonferroni confidence limits ($\hat{w}_i$)		
Year	Species	π_i	u_i	$u_+\pi_i$	o_i	$\hat{w}_i$	B_i	Lower	Upper	$\hat{w}_i$ comps.
1995 (S)	EMS	0.66	0	301.35	0.00	0.00^{NA}	0.00	0.00	0.00	-
	GIS	0.31	62	141.97	0.14	0.44*	0.01	0.30	0.57	a
	WAE	0.01	107	3.24	0.23	33.07*	0.53	25.85	40.30	c
	WHP	0.00	2	0.42	0.00	4.79	0.08	0.00[1]	13.50	-
	YEP	0.03	288	12.03	0.63	23.93*	0.38	21.71	26.16	b
1995 (F)	EMS	0.66	137	204.18	0.44	0.67*	0.00	0.56	0.78	b
	GIS	0.31	48	96.19	0.15	0.50*	0.00	0.33	0.67	a
	WAE	0.01	17	2.19	0.05	7.76*	0.06	3.04	12.47	c
	WHP	0.00	34	0.28	0.11	120.13*	0.87	69.97	170.30	d
	YEP	0.03	75	8.15	0.24	9.20*	0.07	6.81	11.59	c
1996 (S)	EMS	0.97	2	1036.76	0.00	0.00*	0.00	0.00	0.01	-
	GIS	0.01	2	7.15	0.00	0.28*	0.00	0.00[1]	0.79	-
	WAE	0.00	60	4.91	0.06	12.23*	0.15	8.27	16.19	a
	WHP	0.00	1	2.20	0.00	0.45	0.01	0.00[1]	1.63	-
	YEP	0.01	1001	14.99	0.94	66.79*	0.84	65.45	68.13	b
1996 (F)	EMS	0.97	404	569.92	0.69	0.71*	0.03	0.66	0.76	a
	GIS	0.01	0	3.93	0.00	0.00^{NA}	0.00	0.00	0.00	-
	WAE	0.00	18	2.70	0.03	6.67*	0.24	2.68	10.67	b
	WHP	0.00	1	1.21	0.00	0.83	0.03	0.00[1]	2.96	-
	YEP	0.01	163	8.24	0.28	19.78*	0.71	16.39	23.18	c
1997 (S)	EMS	0.99	102	742.08	0.14	0.14*	0.00	0.10	0.17	a
	GIS	0.01	1	4.01	0.00	0.25*	0.00	0.00[1]	0.89	-
	WAE	0.00	23	0.46	0.03	50.39*	0.14	23.70	77.08	b
	WHP	0.00	5	0.26	0.01	19.25	0.05	0.00[1]	41.38	a, b

Year	Species	π_i	u_i	$u_+\pi_i$	o_i	$\hat{w}_i$	B_i	Bonferroni confidence limits ($\hat{w}_i$) Lower	Upper	$\hat{w}_i$ comps.
	YEP	0.00	618	2.19	0.83	281.55*	0.80	269.33	293.77	c
1997 (F)	EMS	0.99	23	196.17	0.12	0.12*	0.00	0.06	0.18	a
	GIS	0.01	1	1.06	0.01	0.94	0.00	0.00[1]	3.37	-
	WAE	0.00	3	0.12	0.02	24.86	0.05	0.00[1]	61.61	-
	WHP	0.00	12	0.07	0.06	174.73*	0.37	48.60	300.87	b
	YEP	0.00	159	0.58	0.80	274.02*	0.58	249.14	298.91	b
1998 (S)	EMS	0.98	8	69.64	0.11	0.11*	0.00	0.02	0.21	a
	GIS	0.01	0	0.36	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	8	0.24	0.11	32.78*	0.24	4.61	60.95	b
	WHP	0.00	1	0.21	0.01	4.71	0.03	0.00[1]	16.77	-
	YEP	0.01	54	0.55	0.76	98.92*	0.72	81.93	115.92	c
1998 (F)	EMS	0.98	13	15.69	0.81	0.83	0.02	0.57	1.09	a
	GIS	0.01	0	0.08	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	1	0.05	0.06	18.18	0.52	0.00[1]	63.61	-
	WHP	0.00	0	0.05	0.00	0.00[NA]	0.00	0.00	0.00	-
	YEP	0.01	2	0.12	0.13	16.26	0.46	0.00[1]	44.00	-
1999 (S)	EMS	0.94	130	697.76	0.17	0.19*	0.00	0.15	0.22	a
	GIS	0.06	0	43.55	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	31	1.39	0.04	22.27*	0.07	12.16	32.37	b
	WHP	0.00	4	1.46	0.01	2.73	0.01	0.00[1]	6.25	-
	YEP	0.00	581	1.84	0.78	316.52*	0.93	300.59	332.46	c
1999 (F)	EMS	0.94	0	8.42	0.00	0.00[NA]	0.00	0.00	0.00	-
	GIS	0.06	0	0.53	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	0	0.02	0.00	0.00[NA]	0.00	0.00	0.00	-
	WHP	0.00	0	0.02	0.00	0.00[NA]	0.00	0.00	0.00	-
	YEP	0.00	9	0.02	1.00	406.4[NA]	1.00	406.41	406.41	a
2000 (S)	EMS	0.72	18	247.41	0.05	0.07*	0.00	0.03	0.12	a
	GIS	0.26	0	90.39	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	47	1.30	0.14	36.21*	0.25	23.55	48.87	c
	WHP	0.00	9	1.15	0.03	7.79*	0.05	1.18	14.41	b
	YEP	0.01	269	2.74	0.78	98.15*	0.69	90.98	105.32	d
2000 (F)	EMS	0.72	0	5.77	0.00	0.00[NA]	0.00	0.00	0.00	-
	GIS	0.26	0	2.11	0.00	0.00[NA]	0.00	0.00	0.00	-
	WAE	0.00	4	0.03	0.50	132.13*	0.68	11.60	252.65	-
	WHP	0.00	0	0.03	0.00	0.00[NA]	0.00	0.00	0.00	-
	YEP	0.01	4	0.06	0.50	62.57*	0.32	5.50	119.65	-
2001 (S)	EMS	0.88	19	318.03	0.05	0.06*	0.00	0.03	0.09	a
	GIS	0.12	0	42.13	0.00	0.00[NA]	0.00	0.00	0.00	-

Year	Species	π_i	u_i	$u_+\pi_i$	o_i	$\hat{w}_i$	B_i	Bonferroni confidence limits ($\hat{w}_i$) Lower	Upper	$\hat{w}_i$ comps.
	WAE	0.00	70	0.44	0.19	158.77*	0.37	114.80	202.75	c
	WHP	0.00	10	0.28	0.03	35.74*	0.08	6.99	64.49	b
	YEP	0.00	263	1.12	0.73	234.96*	0.55	215.41	254.51	d
2001 (F)	EMS	0.88	6	107.18	0.05	0.06*	0.00	0.00	0.11	a
	GIS	0.12	112	14.20	0.92	7.89*	0.30	7.34	8.44	b
	WAE	0.00	0	0.15	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WHP	0.00	1	0.09	0.01	10.60	0.40	0.00[1]	37.85	-
	YEP	0.00	3	0.38	0.02	7.95	0.30	0.00[1]	19.65	-
2002 (S)	EMS	0.88	85	482.21	0.16	0.18*	0.00	0.13	0.22	a
	GIS	0.11	42	61.18	0.08	0.69*	0.00	0.42	0.95	b
	WAE	0.00	93	1.04	0.17	89.34*	0.28	67.56	111.11	d
	WHP	0.00	28	1.06	0.05	26.43*	0.08	13.88	38.98	c
	YEP	0.00	299	1.50	0.55	198.74*	0.63	178.77	218.70	e
2002 (F)	EMS	0.88	11	119.01	0.08	0.09*	0.00	0.02	0.16	a
	GIS	0.11	112	15.10	0.83	7.42*	0.15	6.67	8.16	b
	WAE	0.00	8	0.26	0.06	31.14*	0.63	3.59	58.69	b
	WHP	0.00	0	0.26	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.00	4	0.37	0.03	10.77	0.22	0.00[1]	24.46	-
2003 (S)	EMS	0.81	41	209.91	0.16	0.20*	0.00	0.12	0.27	a
	GIS	0.19	1	48.11	0.00	0.02*	0.00	0.00[1]	0.07	-
	WAE	0.00	61	0.56	0.23	108.35*	0.30	77.04	139.66	c
	WHP	0.00	12	0.82	0.05	14.59*	0.04	3.98	25.21	b
	YEP	0.00	145	0.60	0.56	243.67*	0.66	208.95	278.39	d
2003 (F)	EMS	0.81	0	9.69	0.00	0.00 [NA]	0.00	0.00	0.00	-
	GIS	0.19	10	2.22	0.83	4.50*	0.06	3.00	6.00	a
	WAE	0.00	1	0.03	0.08	38.49	0.48	0.00[1]	133.55	-
	WHP	0.00	0	0.04	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.00	1	0.03	0.08	36.41	0.46	0.00[1]	126.35	-
2004 (F)	EMS	0.79	88	295.90	0.24	0.30*	0.04	0.23	0.37	a
	GIS	0.20	283	75.33	0.76	3.76*	0.53	3.47	4.04	b
	WAE	0.00	0	0.89	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WHP	0.00	0	0.88	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.00	3	1.00	0.01	3.01	0.43	0.00[1]	7.46	-
2005 (S)	EMS	0.63	0	1.88	0.00	0.00 [NA]	0.00	0.00	0.00	-
	GIS	0.36	0	1.07	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WAE	0.00	3	0.01	1.00	422.6 [NA]	1.00	422.59	422.59	-
	WHP	0.01	0	0.03	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.01	0	0.02	0.00	0.00 [NA]	0.00	0.00	0.00	-

Year	Species	π_i	u_i	$u_+\pi_i$	o_i	$\hat{w}_i$	B_i	Bonferroni confidence limits ($\hat{w}_i$) Lower	Upper	$\hat{w}_i$ comps.
2005 (F)	EMS	0.63	20	26.91	0.47	0.74	0.01	0.43	1.06	a
	GIS	0.36	12	15.27	0.28	0.79	0.01	0.29	1.28	a
	WAE	0.00	6	0.10	0.14	58.97*	0.76	1.35	116.58	b
	WHP	0.01	0	0.42	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.01	5	0.29	0.12	17.27	0.22	0.00[1]	36.00	a, b
2006 (S)	EMS	0.64	1	3.22	0.20	0.31	0.01	0.00[1]	1.03	-
	GIS	0.33	2	1.66	0.40	1.20	0.03	0.00[1]	2.90	-
	WAE	0.00	0	0.02	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WHP	0.01	0	0.06	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.01	2	0.05	0.40	42.61	0.97	0.00[1]	102.83	-
2006 (F)	EMS	0.64	2	209.72	0.01	0.01*	0.00	0.00[1]	0.03	-
	GIS	0.33	314	108.50	0.96	2.89*	0.47	2.81	2.97	a
	WAE	0.00	0	1.04	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WHP	0.01	0	3.68	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.01	10	3.06	0.03	3.27	0.53	0.64	5.89	a
2007 (S)	EMS	0.29	0	3.44	0.00	0.00 [NA]	0.00	0.00	0.00	-
	GIS	0.65	1	7.79	0.08	0.13*	0.00	0.00[1]	0.45	-
	WAE	0.01	0	0.11	0.00	0.00 [NA]	0.00	0.00	0.00	-
	WHP	0.03	2	0.32	0.17	6.26	0.19	0.00[1]	16.68	-
	YEP	0.03	9	0.35	0.75	26.01*	0.80	14.83	37.19	a
2007 (F)	EMS	0.29	43	88.83	0.14	0.48*	0.08	0.31	0.66	a
	GIS	0.65	250	201.12	0.81	1.24*	0.22	1.15	1.33	b
	WAE	0.01	9	2.86	0.03	3.15	0.55	0.48	5.82	b
	WHP	0.03	0	8.26	0.00	0.00 [NA]	0.00	0.00	0.00	-
	YEP	0.03	8	8.94	0.03	0.89	0.16	0.09	1.70	a, b
2008 (S)	EMS	0.79	0	27.74	0.00	0.00 [NA]	0.00	0.00	0.00	-
	GIS	0.20	24	6.94	0.69	3.46*	0.02	2.44	4.48	a
	WAE	0.00	2	0.03	0.06	70.67	0.34	0.00[1]	195.84	-
	WHP	0.00	6	0.05	0.17	121.29*	0.58	5.00	237.58	b
	YEP	0.01	3	0.24	0.09	12.37	0.06	0.00[1]	29.99	-
2008 (F)	EMS	0.79	126	1470.03	0.07	0.09*	0.01	0.07	0.10	a
	GIS	0.20	1685	368.00	0.91	4.58*	0.38	4.49	4.67	c
	WAE	0.00	5	1.50	0.00	3.33	0.28	0.00[1]	7.17	a, b, c
	WHP	0.00	3	2.62	0.00	1.14	0.10	0.00[1]	2.85	-
	YEP	0.01	36	12.85	0.02	2.80*	0.23	1.61	3.99	b
2009 (S)	EMS	0.29	1	29.90	0.01	0.03*	0.00	0.00[1]	0.12	-
	GIS	0.69	3	70.76	0.03	0.04*	0.00	0.00[1]	0.10	-
	WAE	0.00	4	0.33	0.04	11.97	0.06	0.00[1]	27.11	-

Year	Species	π_i	u_i	$u_+\pi_i$	o_i	$\hat{w}_i$	B_i	Bonferroni confidence limits ($\hat{w}_i$) Lower	Upper	$\hat{w}_i$ comps.
	WHP	0.00	8	0.47	0.08	17.03*	0.09	2.12	31.95	a
	YEP	0.01	86	0.54	0.84	158.75*	0.85	141.26	176.24	b
2009 (F)	EMS	0.29	40	215.43	0.05	0.19*	0.02	0.11	0.26	a
	GIS	0.69	658	509.87	0.90	1.29*	0.11	1.25	1.33	b
	WAE	0.00	7	2.41	0.01	2.91	0.24	0.09	5.73	a, b, c
	WHP	0.00	3	3.38	0.00	0.89	0.07	0.00[1]	2.20	-
	YEP	0.01	27	3.90	0.04	6.92*	0.57	3.55	10.29	c

[1]Negative lower limits were changed to 0.00.

CHAPTER 3

IMPACT OF PREDATOR MANAGEMENT ON PREY ABUNDANCE: DID CORMORANT MANAGEMENT RESULT IN INCREASED WALLEYE AND YELLOW PERCH POPULATIONS IN ONIEDA LAKE, NY?

Anticipated authorship for peer-reviewed manuscript:
Robin L. DeBruyne, Jeremy T. H. Coleman, Lars G. Rudstam, James R. Jackson, Anthony J. VanDeValk, Milo E. Richmond, and Travis L. DeVault

ABSTRACT

Piscivorous birds, such as double-crested cormorants (*Phalacrocorax auritus*), are top predators that have been found to significantly affect their prey in some locations. Oneida Lake, New York, experienced a decline in the walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) adult populations in the 1990s which was attributed to decreased age-1 recruitment and increased subadult mortality from increased cormorant predation. Non-lethal cormorant management was initiated in 1998 and intensified in 2004 to reduce the subadult mortality of percids and increase the adult percid populations. In this study, we evaluate the response of the walleye and yellow perch populations to the decreased cormorant abundance resulting from management actions. Cormorant consumption of percids decreased with decreased cormorant abundance and when age-0 gizzard shad (*Dorosoma cepedianum*) were present. Subadult mortality for both percid species decreased when cormorant abundance was reduced to pre-1989 levels. Adult walleye population increased with cormorant management but this increase was only partly explained by decreased subadult mortality; decreased adult mortality, likely associated with more restrictive harvest regulations, contributed more to the increase. The adult yellow perch population did not responded as strongly as walleye, likely

due to decreased age-1 recruitment caused by factors other than cormorants. This whole-lake predator removal experiment had the desired results for the walleye population (decreased subadult mortality, increased adult abundance to 400,000), but not completely for yellow perch (only decreased subadult mortality). Confounding factors in the experiment were the diet shifts observed for cormorants to age-0 gizzard shad which likely resulted in a faster response to partial cormorant management than predicted and the decreased age-1 recruitment for yellow perch likely due to other ecological changes in the lake independent of cormorant management. Future cormorant management actions should consider and incorporate these factors through diet monitoring of cormorants and other predators.

INTRODUCTION

Large-scale ecological change may arise from natural perturbation to a system or as a result of human activity, such as deliberate stocking or introduction of a species. The Great Lakes region has experienced a dramatic increase in the number of piscivorous double-crested cormorants (*Phalacrocorax auritus*; hereafter cormorants) since the 1970s due to the cessation of DDT use and human persecution, and possibly increases in forage base (Hatch 1995; Weseloh et al. 2002). The regional cormorant population increase resulted in concern about potential impacts on fish communities near breeding colonies, within migratory routes, and near winter roosting areas. Cormorants consume approximately 20-30% of their body weight in fish/day (Glahn and Brugger 1995; Schultz et al. 2013) and when abundant this predation could adversely affect fish communities, including sport fish and their prey. Even though cormorants generally consume smaller fish than targeted by sport fisheries and therefore are not in direct competition with anglers (VanDeValk et al. 2002; Barks et al. 2010; Ridgeway et al. 2012), there are locations where significant negative effects on sportfish populations have been demonstrated. Cormorants foraging on Oneida Lake, New York were shown to significantly affect walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*)

populations (VanDeValk et al. 2002; Rudstam et al. 2004). Cormorants nesting in Lake Ontario were found to negatively affect smallmouth bass (*Micropterus dolomieu*) and yellow perch populations (Burnett et al. 2002; Lantry et al. 2002). Cormorant colonies in the Le Cheaneaux Islands in northern Lake Huron have been implicated in declines in yellow perch populations in some studies (Fielder 2008, 2010), but not in others (Diana et al. 2006). This potential to negatively affect fishery resources (Ashmole 1963; Birt et al. 1987; Cowx 2003) propelled the need to better understand the impacts of cormorant predation on their prey in the Great Lakes region.

Cormorant diet composition varies temporally and geographically (Neuman et al. 1997; Wires et al. 2001; Johnson et al. 2010; DeBruyne et al. 2012, 2013; Hundt et al. 2013), suggesting that cormorant effects on fish populations may not be consistent across systems. In some locations, cormorant prey consumption shifted with changes in available prey or establishment of non-native species, such as round goby (*Neogobius melanostomus*) or gizzard shad (*Dorosoma cepedianum*), resulting in reductions in consumption of sport or other native species (Johnson et al. 2010; Coleman et al. 2012; DeBruyne et al. 2012, 2013). Therefore the actual impact of cormorants on sportfish populations may depend on the fish community present, not only on the number of cormorants. This emphasizes the need to fully evaluate the actual, not only potential, effect cormorants have on local fish populations and to clarify the role of cormorants within local ecosystems.

Due to a variety of reasons (e.g., real or perceived negative effects on fish populations, destruction of vegetation, negative effects on co-nesting waterbirds), management of cormorants occurs at multiple breeding, migration, and wintering locations within North America (Wires et al. 2001). Forms of cormorant management include nesting attractants or deterrents to encourage or discourage nesting in specific locations, nest destruction, egg oiling, and non-lethal harassment and lethal culling at foraging, loafing and nesting locations (Tobin et al. 2002; Dorr et al. 2010a, b; DeVault et al. 2012). Management action aimed at

protecting co-nesting waterbirds or vegetation can be assessed for effectiveness through monitoring of the other waterbirds and vegetation (Farquhar et al. 2012; Hebert et al. 2014). However assessing the effectiveness of management aimed at protecting fishery resources is more difficult. Because cormorants typically consume sportfish at smaller sizes (i.e., prior to recruitment to commercial or recreational fisheries), impacts of cormorants can be confounded by other factors that contribute to mortality of subadults (other predators, starvation, suboptimal weather conditions). In addition, data on subadult fish mortality are rare.

One of the most thoroughly studied aquatic predator-prey systems is that of Oneida Lake, New York. Early work focused on walleye and yellow perch (together referred to as percids hereafter) and the interactions between these two species (Forney 1980). In the early 1990s, the system began to undergo substantial ecological changes, which altered the trophic dynamics in the lake (Miehls et al. 2009). Changes in nutrients, water clarity, and benthic communities associated with the zebra mussel (*Dreissena polymorpha*) invasion affected the ecosystem from the bottom-up (Idrisi et al. 2001; Mayer et al. 2002; Zhu et al. 2006) while predation from cormorants affected the system from the top-down (Rudstam et al. 2004; Irwin et al. 2008); resulting in a dramatic decrease in the adult percid populations beginning in 1991. Rudstam et al. (2004) through a weight-of-evidence approach concluded that cormorants were likely responsible for the observed declines in yellow perch adult abundance and that cormorant predation, combined with decreased age-1 walleye abundance, was responsible for decreased adult walleye population. The evidence for their conclusions was as follows: (1) the arrival of cormorants coincided with the percid populations decline; (2) there was an increase in subadult percid mortality; and (3) the number of percids calculated to be missing from the population was similar to the number of percids removed through cormorant predation (Rudstam et al. 2004). Based on these conclusions, cormorant management was implemented on Oneida Lake with the goal of decreasing subadult mortality and increasing

the adult percid populations.

The continuation of systematic data collection on Oneida Lake provides a rare and valuable opportunity to analyze the response of two percid species to cormorant predation. Our goal was to determine if decreasing the cormorant population of Oneida Lake decreased percid subadult mortality and reversed the declining trend in adult abundances observed during the 1990s (Rudstam et al. 2004). First we document changes in cormorant feeding days as a response to management actions. Second, we investigate if walleye and yellow perch subadult mortality declined after cormorant management and how the estimated number of these two fish species consumed by cormorants compared to the numbers predicted and observed to recruit to the adult population. If cormorants were significant contributors to the increase in subadult mortality in the 1990s as concluded by Rudstam et al. (2004) rather than a response to other ecosystem changes in Oneida Lake, we expect that subadult mortality should decline to levels similar to the pre-cormorant years (1975-1989). We also expect cormorant feeding days to be a significant variable for predicting recruitment from age-1 to adult. Finally, we analyzed the changes in abundance of the two percid species following cormorant management and estimated the potential importance of cormorant management contributing to these changes. This analysis revisits the conclusions of Rudstam et al. (2004) using a decade of additional data on the two percid species. Earlier analyses of the effect of the cormorants on Oneida Lake (VanDeValk et al. 2002; Rudstam et al. 2004; Irwin et al. 2008) may have been influenced by the zebra mussel invasion and associated increases in water clarity and macrophyte coverages (Idrisi et al. 2001; Zhu et al. 2006) which occurred simultaneously with increases in cormorant abundance; however, these potentially confounding ecosystem variables should not complicate this analysis because they have remained relatively constant during the 2000s (Jackson et al. 2012).

METHODS

Study Site

Oneida Lake is a shallow, moderately productive lake with a surface area of 207 km^2 (Mills et al. 1978; Figure 3.1). Oneida Lake is the largest lake contained entirely within the State of New York and has a valuable recreational fishery for walleye, yellow perch, smallmouth bass and largemouth bass (*M. salmoides*) (Connelly and Brown 1991; VanDeValk et al., in press). Zebra mussels were discovered in the lake in 1991 and quagga mussels (*D. rostriformis bugensis*) arrived around 2005 (Mills et al., in press). The colonization of the lake by zebra mussels was followed by increased water clarity (Idrisi et al. 2001), increased macrophyte coverage (Zhu et al. 2006), and changes in the benthic community (Mayer et al. 2002, in press).

Double-crested cormorants first nested on Oneida Lake in 1984 (Claypoole 1988). Nest counts increased steadily from 1984, peaking at 365 nests in 2000 (Coleman 2009). Migrating cormorants stop-over on Oneida Lake, and are present on the lake from August through October. Total daily abundances increased over time and were found to exceed 2000 individuals in 1996 and 1997 (Rudstam et al. 2004; Coleman 2009). Cormorant management was initiated in 1991 with a series of progressively more restrictive management actions enacted through 2009. From 1991-1997, management largely focused on restricting nesting locations to specific island locations on the lake. Control actions were escalated from 1998-2003 when the colony was limited to 100 active nests through nest destruction and egg oiling, coupled with a non-lethal harassment program designed to move all cormorants off the lake starting around September 1. From 2004-2009, cormorant management consisted of non-lethal harassment through the entire breeding and migration seasons (April-September/October, excluding May), limited lethal take, nest destruction, and egg oiling of all nests on the lake (further cormorant management details can be found in in Coleman 2009 and DeVault et al. 2012).

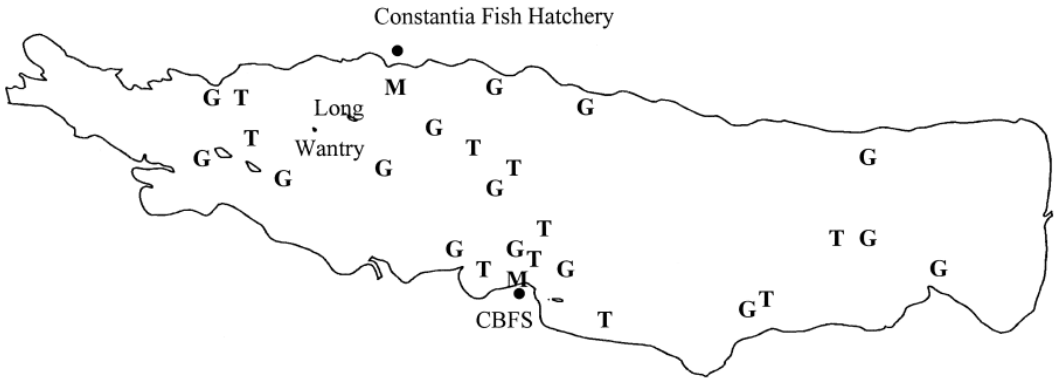


Figure 3.1. Map of Oneida Lake, New York, USA, indicating netting sites used for marking walleye and yellow perch (M), trawl sites used for the age-1 catch per effort index (T), gill net sites used for weekly adult community sampling (G), and the two cormorant nesting islands (Wantry and Long Islands). CBFS indicates the location of the Cornell Biological Field Station.

Cormorants

Abundance: Cormorants on Oneida Lake were counted at least once per week most weeks from mid-April through October from 1995-2009. The entire lake was surveyed to account for all known or potential roosting and loafing locations, providing weekly lake-wide abundance estimates. Counts were performed by either trained staff from the Cornell Biological Field Station (1995-2003) or USDA Animal and Plant Health Inspection Service (APHIS), Wildlife Services (2004-2009) personnel at dawn or dusk. All counts were conducted either Sunday (1998-2003) or Monday (2004-2009) prior to any weekly hazing activities on the lake. Cormorant counts were categorized into adults and chicks. Chicks were counted during weekly nest monitoring at the nesting colonies. Beginning in late June, fledgling chicks were counted as adults during the weekly census. No eggs were permitted to hatch from 2004-2009. Migrant cormorants typically began to arrive in late July.

To describe the total cormorant foraging pressure on Oneida Lake, we incorporated all weekly counts into a single metric, cormorant feeding days. Each cormorant feeding day represents a consumption of 456 g fish based on an assumed consumption of 20% of body weight per day and the weights of cormorants collected on Oneida Lake during diet sampling in 1995 and 1996 (Rudstam et al. 2004). Resident adult, subadult, fledged chicks and non-resident migrants were assigned as 1 feeding day for each day the birds were present on the lake. Prior to the fledgling stage, chicks were assumed to consume 71% of the adult consumption per day (Fowle 1997), therefore each chick was assigned 0.71·adult feeding day consumption for each day present. Cormorant feeding days were then combined with diet data to estimate prey-specific foraging by cormorants during each year. Only counts of resident birds and chicks produced were available for Oneida Lake prior to 1995. Therefore, the number of migrant cormorants on the lake was estimated using a model regressing the number of breeding adults in Lake Ontario (representing the regional population of likely migrants to Oneida Lake) with the few migrant counts which were available prior to 1995

(1979, 1987, 1993) and the maximum migrant counts from 1995-1997 ($r^2 = 0.89$; further details in Coleman 2009). These estimated migrant counts were combined with the breeding season counts on Oneida Lake to obtain the total number of cormorant feeding days from 1978-1994.

Diet and Consumption: Chick regurgitant samples were collected in 1995–1996 and 1998–2003, pellets were collected in 1997, and whole birds (stomachs) were collected in 1995–1996 and 2001–2009. Diet items from regurgitant and stomach samples were identified to lowest possible taxon and measured when possible. Scales were taken from fish for age determination. The mean length for that species and age group in the diet or the mean length-at-age for that species in the lake was assigned to the diet item when the length could not be estimated (Cornell Biological Field Station, *unpublished data*). Weights of individual fish were estimated using length-weight regressions developed from gillnet and trawl surveys conducted on Oneida Lake when available (Cornell Biological Field Station, *unpublished data*) or from length-weight regressions published elsewhere (Schneider et al. 2000). Analysis of pellets for 1997 is described in detail in VanDeValk et al. (2002). Taxa were identified based on otoliths and bones found in the pellets (Hansel et al. 1988), and age of walleye and yellow perch in diets was inferred from length regressions of fish length to otolith. Diets were temporally categorized into summer (15Apr – 31Jul) and fall (01Aug – 31Oct) diets. Spring diets (April/May) were combined into summer diets due to similarity and small sample sizes. Further detailed diet analysis methods and results for 1995-2009 can be found in DeBruyne et al. (2013).

Prey-specific cormorant consumption was calculated by multiplying the diet composition (by mass) of a prey species with the estimated total consumption by cormorants for that given year and season. Age-specific walleye and yellow perch consumption was calculated from the numerical proportion of each age class present in the diets (by mass) and total biomass of percids consumed. The total biomass of each age class consumed was

divided by the mean mass per individual (by season) to obtain the number of individuals consumed for a year and season. Age-1 percids consumed prior to Aug 1 (summer season diets) were not included in the total subadults consumed because the age-1 indices for walleye and yellow perch are based on catches later in the year (Aug 1 occurring approximately in the middle of indices: gillnets from June-September, trawls from July-October, see *Percid Abundance* methods below). Age-1 percids consumed during the summer season would therefore have been removed from the population prior to time we obtain the age-1 indices used here and will therefore not affect the adult recruitment predictions (see *Percid Abundance: Subadult Mortality Analysis* methods below) and including those fish in the consumption comparisons would overestimate the subadult mortality attributable to cormorant predation. The number of subadults consumed (age 1 in the fall and age 2 and age 3 for walleye, age 1 in the fall and age 2 for yellow perch) was compared to the number of predicted and observed age-3 yellow perch and age-4 walleye abundances for the 1999-2007/2008 year classes (1993-1998 percid year class consumption can be found in Rudstam et al. [2004]). If cormorants were responsible for any decreased adult recruitment (from consumption of subadults) then the number consumed and observed would equal the number predicted.

Percid Abundance

Adults: Annual sampling of adult percids in Oneida Lake has occurred since the 1950s using graded, multifilament gillnets. Standardized methods were used every year with few exceptions (detailed description in Irwin et al. 2008). Gillnets were set at 15 standard locations and in a fixed sequence, one location each week for 15 weeks (June-September; Figure 3.1). Densities of adult walleye (≥ age 4) were estimated from mark-recapture population estimates which occurred in 24 years since 1957, where adult densities in intervening years were approximated from the mortality between successive population

estimates. More details of percid mark-recapture methods are available in VanDeValk et al. (2002) and Irwin et al. (2008). Adult walleye abundance from 1978-1987 and 1992-1994, when no mark-recapture experiments were conducted, was estimated from age-structured, non-linear model which combined mark-recapture estimates, gillnet and trawl catches over the time series (Irwin et al. 2008). Adult (≥ age 3) yellow perch mark-recapture population estimates have been conducted 11 non-consecutive years since 1969. The relationship between concurrent age-specific gillnet catch and mark-recapture density estimates was used to assign gillnet corrected catches and develop age-specific gillnet selectivities and abundances for age-2 and older yellow perch during all years (Rudstam and Jackson 2012a). All percid density estimates by age were considered the densities in April. Data are available online (Rudstam and Jackson 2012 a, b)

Change point analysis (Change-Point Analyzer 2.3 software; Taylor Enterprises, Libertyville, Ill) was used to determine if shifts in percid abundances were evident over time and to explore the effectiveness of cormorant management in increasing the adult percid populations. The program uses 1000 random bootstraps to assess if changes over time in percid abundances were significant compared to changes due to random chance. If significant changes were identified, data were blocked according to the change point analysis and tested using t-test (1 pivot identified) or analysis of variance (>1 pivot identified) to further examine the differences between identified year ranges. Alpha <0.05 was considered significant.

Yearlings: Densities of age-1 yellow perch were calculated as the catch-per-unit-effort (CPUE) of the 5.5m bottom trawls which occurred from July-October at 10 standard sites (approximately 130-150 hauls/year; Figure 3.1) given the area swept by the bottom trawl is known ($0.1 ha \cdot haul^{-1}$; Forney 1977) and a catchability assumed to be 1.0. Lengths of fish captured in bottom trawl sampling were recorded and scale samples were taken for age determination. The ratio of subadult walleye catches in the bottom trawl to catches in gillnet has shifted since late 1990s (Rudstam and Jackson 2012b), leading to a change of methods

traditionally used to assess the density of subadult walleye, particularly age-1 walleye, compared to methods presented in Rudstam et al. (2004). Catches of age-1 walleye are now comparatively lower in the bottom trawl and no longer correlate as well with age-4 walleye abundance for the same year class. Therefore, densities of age-1 walleye were estimated from averaging the 5.5m bottom trawl CPUE and gillnet catches after applying gear- and age-specific catchabilities developed by Irwin et al. (2008).

Subadult Mortality Analysis: Rudstam et al. (2004) documented the change in the percid recruitment relationship from age-1 to adults (age 3 yellow perch, age 4 walleye) and hypothesized the relationship would return to the pre-1989 equation if the additional mortality caused by cormorants on subadult percids was eliminated. We assessed this hypothesis by grouping year classes based on the potential cormorant predation pressure specific year classes of percids were exposed to on Oneida Lake and testing for differences between regression models for those year-class groupings. The year-class groupings were: 1960-1988, 1989-2002, 2003-2007 (walleye), 2003-2008 (yellow perch). The 1960-1988 year classes did not have increased mortality due to cormorants on Oneida Lake; the 1989-2002 year classes would have experienced significant predation as a result of cormorant foraging on Oneida Lake; and the 2003-2007/2008 year classes of percids experienced reduced cormorant predation as the number of cormorant feeding days returned to pre-1989 levels. If the cohorts from 2003-2007/2008 experienced reduced subadult mortality, the regression describing their recruitment patterns would return to the pre-cormorant relationship. Analysis of covariance (ANCOVA) was performed using the year-class groupings to test for changes in the recruitment relationships between age-1 indices and adult percids based on the presence of cormorants, with age-1 abundance as the covariate. Age-1 and adult percid densities were natural log transformed to better meet regression assumptions. Year-class groupings were compared using Bonferroni correction for multiple comparisons.

The resulting ANCOVA regression equations predicting age-4 walleye and age-3

yellow perch abundance for the 1960-1988 year classes were used to predict the number of expected adult recruits for the 1999-2007/2008 year classes. These predicted abundances were then compared with the observed number of recruits and cormorant consumption of that year class (see *Cormorants: Diet and Consumption* methods above). Other sources of subadult mortality are incorporated into the predictive model providing the number of age-3 or 4 percids and we assumed that these other sources of mortality were constant over time and additive.

We also used Akaike's Information Criterion corrected for small sample size (AIC_c) to select the regression models which best explained the percid recruitment observed in Oneida Lake for year classes 1960-2007/2008. By including other predictors in addition to age-1 abundance indices, it may be possible to identify other sources of variation in percid recruitment in Oneida Lake and what factors may affect it. For example, if cormorants significantly influenced the recruitment of percids in Oneida Lake, then AIC_c model selection should incorporate cormorant abundance into a high ranking model(s), even though their effect is recent and possibly short-term. If age-1 indices were left out of the top model(s), it could suggest the need to reconsider which indices are used to predict adult recruitment. Predictors included in candidate models were ln(age-1 trawl CPUE) (yellow perch only), ln(age-2 trawl CPUE), ln(age-2 gillnet density), ln(age-1 combined gear density) (walleye only), and total cormorant feeding days experienced by age 1 and 2. All statistical tests were done using SAS 9.2.

Percid Adult Population Simulation

Walleye: Simulation modeling (1992-2020) was used to explore the effect of variable subadult recruitment and adult mortality on adult percid population abundances. Because only increasing adult recruitment, the expected result of cormorant removal, did not explain the observed pattern in adult walleye densities, additional scenarios were examined to reveal what

further changes in population characteristics were required to accurately reflect the observed pattern in adult percid densities. By altering additional population characteristics (i.e., adult mortality), while using empirical data for characteristics where available, additional current and past influences on the adult population could be identified (Table 3.7 lists scenarios, parameter estimates, empirical data used to derive estimates, and years specific estimates were used during simulations). The first simulation (Scenario 1) explored used mean historical (1964-1991) adult survival and age-4 recruitment information to depict what would have been expected, on average, if there had been no ecological change on the lake. Scenario 2 simulated the adult population if cormorant management had not occurred on the lake, with historical survival (0.70) and the mean age-4 recruitment during increased predation years (1992-2001). Scenario 3 used the historical adult survival and varied the age-4 recruitment associated with cormorant management; using the mean recruitment during increased predation years from 1992-2001 and during lowered predation years from 2002-2011. If increased subadult mortality was the major factor suppressing the adult population through decreased age-4 recruitment, then this scenario would mimic the empirical data. Scenario 4 used the changes in age-4 recruitment associated with cormorant presence (as above), but increased adult survival during 2000-2003 in association with an increase in the minimum harvest size (from minimum of 15" to 18") and decreased daily bag limit (from 5 to 3 fish/day) which was in effect from 2000-2003. After 2003, the survival reverted to 0.70 to simulate the walleye population response to a short-term harvest regulation change. Scenario 5 was the same as Scenario 4 except the adult survival was only reduced to 0.85 (mean adult survival 2004-2011) from 2004-2020 in association with the walleye harvest regulation changes which began in 2004 returning the minimum size to 15", but continued the 3 fish/day bag limit to simulate the walleye population response to long-term harvest regulation changes. The last scenario examined, Scenario 6, simulates the walleye population under reduced age-3 recruitment and the observed changes in harvest regulations of Scenario 5. This last scenario

was done to explore a situation with no cormorant management and only walleye harvest management.

Yellow Perch: Scenario 1 used the mean historical (1964-1991) adult survival (0.67) and age-3 recruitment information to depict what would have been expected, on average, if there had been no ecological changes on the lake. Scenario 2 simulated the adult population if cormorant management had not occurred on the lake, with adult survival 0.75 (mean survival 1992-2004) and the mean age-3 recruitment during increased predation years (1992-2004). Scenario 3 used the historical adult survival and the mean age-3 recruitment during increased predation years (1992-2004) and lowered predation years (2005-2011). If decreased age-3 recruitment, resulting from cormorant predation, was the most influential factor determining adult abundance then removing cormorants should increase adult yellow perch abundance (observed data) and therefore Scenario 3 should result in similar population trajectory as the observed data. Scenario 4 used the changes in age-3 recruitment associated with cormorant presence (as above), but adult survival varied from 1992-2004 and 2005-2020 to 0.75 and 0.71 (mean adult survival 2005-2011), respectively, reflecting the changes in estimated population survival during those years.

RESULTS

Cormorants

Abundance: Total cormorant feeding days increased rapidly from the late 1970s through 1997 similar to the overall Great Lakes region cormorant population (Weseloh et al. 2002) and the Oneida Lake resident population (Rudstam et al. 2004) (Figure 3.2). Total and fall cormorant feeding days decreased from the highest level in 1997 (prior to hazing) until 2005 when feeding days remained relatively stable at low levels (fall mean = 13,700 feeding days 2005-2009) compared with those estimated during the 1990s (fall mean = 75,425 feeding days 1995-1999; Table 3.1; Figure 3.2). Summer cormorant feeding days remained stable

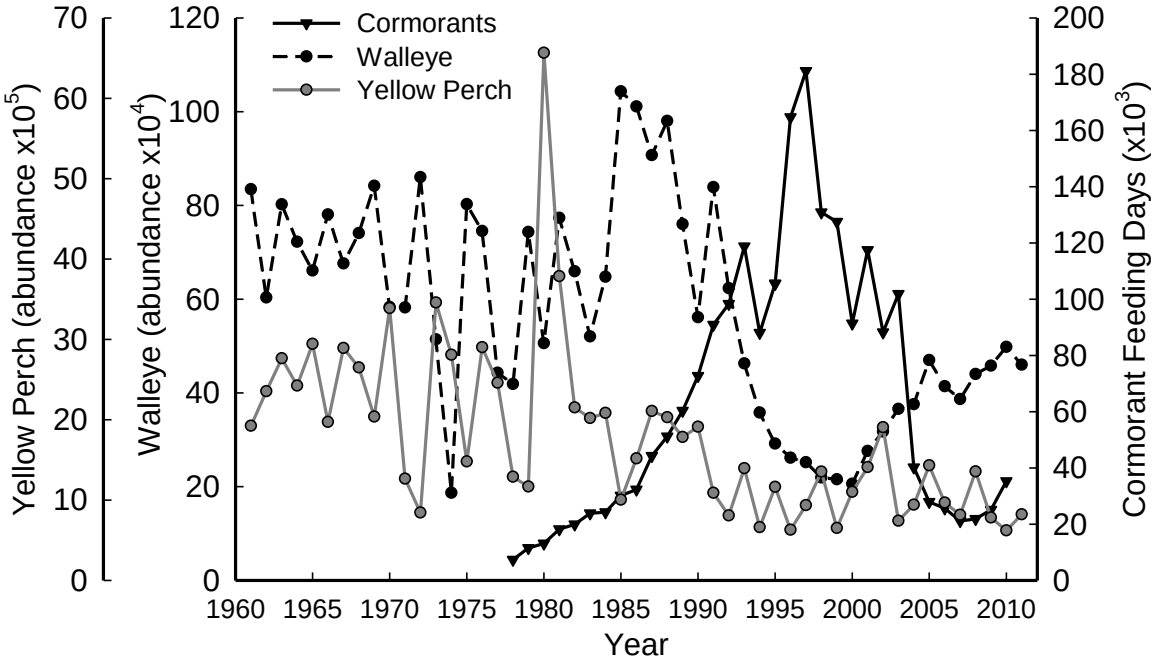


Figure 3.2. Adult walleye (≥ age 4) and yellow perch (≥ age 3) abundances and estimated total cormorant feeding days for Oneida Lake, NY, 1960-2011. See methods for specifics of each species' abundance calculation.

Table 3.1. Cormorant feeding days during summer (April-July) and fall (August-October) from 1995-2009 on Oneida Lake, NY. (*) denotes hazing occurred during given season.

Year	Summer	Fall	Total
1995	37555	67944	105499
1996	59787	104932	164719
1997	73663	107469	181131
1998	80552	50360*	130911
1999	81099	46424*	127523
2000	56746	34569*	91315
2001	68558	48909*	117467
2002	56811	31388*	88199
2003	70087	31760*	101847
2004	23421*	16783*	40204
2005	16086*	11822*	27908
2006	9291*	16320*	25611
2007	9008*	12101*	21109
2008	7248*	14615*	21863
2009	11499*	13643*	25142

(mean = 64,984 feeding days 1995-2003) until summer hazing began in 2004, then summer cormorant feeding days declined (mean = 12,758 feeding days 2004-2009; Table 3.1).

Diet and Consumption: Cormorant diet composition from 1995-2009 is presented in detail in DeBruyne et al. (2013). The ten species with the highest overall percent by weight were (in order) yellow perch, walleye, gizzard shad, *Lepomis* spp., burbot (*Lota lota*), white perch (*Morone americana*), white sucker (*Catostomus commersonii*), rock bass (*Ambloplites rupestris*), smallmouth bass, and logperch (*Percina carprodes*) (Appendix II). Diet composition was highly variable across years and seasons. Notable weight contributions by species other than the ten listed above included emerald shiner (*Notropis antherinodes*) in fall 1996 (4.2%) and fall 1998 (21.8%); brown bullhead (*Ameiurus nebulosus*) in summer 1995 (6.5%); and *Esox* spp. during the summer and fall of 2008 (5.3 and 4.0%, respectively). Total biomass of the top three prey items consumed by season and year changed over time (Figure 3.3). Total biomass consumed decreased from a maximum of 79,154 kg in 1997 to 9,225 kg in 2007. Simultaneous with the decline in overall biomass consumed, the prey composition shifted in the fall to be dominated by gizzard shad in most years since 2001 (Figure 3.3).

The number of subadult percids consumed by cormorants declined over time (Table 3.2). Cormorants consumed over 212,000 subadult walleye in 1998, however the average number of subadult walleye consumed from 2007-2009 was only 2,600 individuals. Consumption of subadult yellow perch peaked in 1999 with 1.56 million subadult yellow perch being consumed by cormorants. Cormorant consumption of subadult yellow perch sharply declined after 2005 with the mean number of individuals consumed from 2005-2009 at 15,228 individuals.

Percid Abundance

Adults: Adult percid abundance generally increased after the start of cormorant management in 1998 on Oneida Lake, compared to mid-1990s abundances (Figure 3.2)

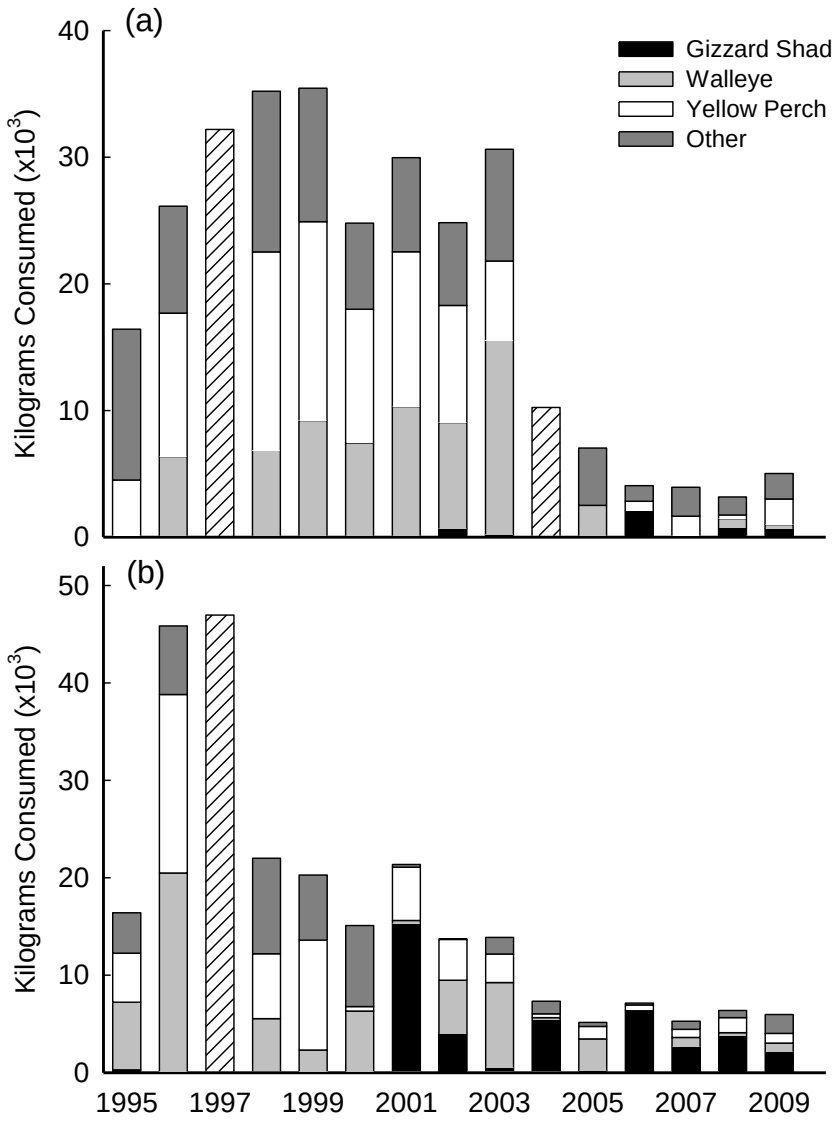


Figure 3.3. Total cormorant biomass consumption by year in Oneida Lake during (a) summer and (b) fall. Dashed bars indicate no total diet breakdown available for that season (no weight estimates available in 1997, no samples taken in summer 2004), however total biomass consumed estimated from seasonal cormorant feeding days. Note different y-axes. Data from DeBruyne et al. (2013). See VanDeValk et al. (2002) and Rudstam et al. (2004) for percid-specific consumption in 1997.

Table 3.2. Estimated number of subadult walleye and yellow perch (by age) consumed by cormorants in Oneida Lake, 1998-2009. S=summer, F=fall.

		Walleye Age Class					Yellow Perch Age Class			
Year		0	1	2	3	4+	0	1	2	3+
1998	S	3987	11960	3987	11960	3987	67773	139532	11960	63786
	F	0	184462	0	0	0	0	368925	0	0
1999	S	0	26986	21589	5397	1799	0	890544	93552	61169
	F	64515	0	0	0	0	258059	580633	0	0
2000	S	0	16177	14706	3677	0	3387	102979	38617	40650
	F	20936	13957	13957		0	0	27915	0	0
2001	S	47045	17474	20162	6049	3360	207671	104172	30915	41669
	F	22550	0	0	0	0	236777	0	11275	22550
2002	S	493	19237	18744	7892	0	0	99639	10852	36995
	F	5344	32065	5344	5344	0	16032	5344	0	16032
2003	S	0	16866	53194	9082	0	0	142716	25948	19461
	F	0	0	0	0	12725	0	0	0	12725
2004	F	9174	0	0	0	0	11009	0	0	1835
2005	S	0	42467	0	0	0	0	0	0	0
	F	12669	0	2534	2534	2534	45607	10135	0	2534
2006	S	0	0	0	0	0	0	0	5145	5145
	F	0	0	0	0	0	13801	12421	1380	0
2007	S	0	0	0	0	0	0	0	0	11148
	F	785	1177	0	1177	1177	22980	978	0	2445
2008	S	0	0	0	1129	0	2258	0	0	1694
	F	723	362	1085	0	0	24153	3605	3605	5768
2009	S	0	517	517	517	517	0	25244	7920	9405
	F	0	439	877	0	1754	44456	4894	816	3671

although both percid population levels were below historical (pre-1990) population levels in 2010. Adult walleye population levels have increased since 1998 (compared to early 1990s) and have remained slightly above 400,000 individuals from 2005 to 2010. Change point analysis indicates four shifts in abundance in the time series (Table 3.3). Two of the shifts were detected with 100% confidence, one at 1998 and the other at 2001. Blocking the walleye data into four blocks accounting for changes detected with at least 95% confidence (1959-1984, 1985-1992, 1993-2002, 2003-2009) and performing an analysis of variance test, with Tukey's multiple comparisons tests, indicated periods were significantly different ($P < 0.0001$) and all multiple comparisons were significant except 1993-2002 vs. 2003-2009. Catches of adult yellow perch were at the lowest levels in 1996 and have been variable, with no significant trend after 2003. The corresponding population abundance averaged approximately 940,000 adults from 2003-2011. Change point analysis indicated only one significant change was evident in the adult yellow perch abundance during our time series (1991) although the confidence limits for this change point are large (Table 3.3). Perch abundance was significantly greater pre-1990 (2.28 million individuals) than 1991-2010 (1.02 million individuals, t-test, $P <0.001$).

Yearlings: Age-1 index of walleye density showed two strong year classes in 1997 and 2001, but declined and remained low after 2003 (Figure 3.4) (Student's t-test 1989-1999 YC vs. 2000-2007 YC, equal variances, DF = 17, $P > 0.05$). Yellow perch age-1 bottom trawl CPUE increased in 1999, but has since declined significantly (Figure 3.4) (Student's t-test 1989-1999 YC vs. 2000-2008 YC, unequal variances, DF = 10.3, $P = 0.016$). There have been no substantial walleye age-1 cohorts since the 2002 year class or yellow perch age-1 cohorts since the 1998 year class.

Subadult Mortality Analysis: The walleye ANCOVA model was found to be significant overall ($P < 0.0001$) and both model factors (age-1 index and year-class grouping based on cormorant abundance) were also significant (Table 3.4). Recruitment predictions

Table 3.3. Change point analysis statistics for time trend analysis of percid adult densities in Oneida Lake, 1960-2010.

Species	Pivot Year	95% CI	Confidence Level (%)	Start Abundance ($x10^4$)	End Abundance ($x10^4$)
Yellow Perch	1991	1960, 1992	100	228.01	102.71
Walleye	1985	1973, 1985	95	67.25	98.53
	1989	1989, 1990	92	98.53	69.57
	1993	1993, 1993	100	69.57	28.59
	2003	2000, 2003	100	28.59	42.97

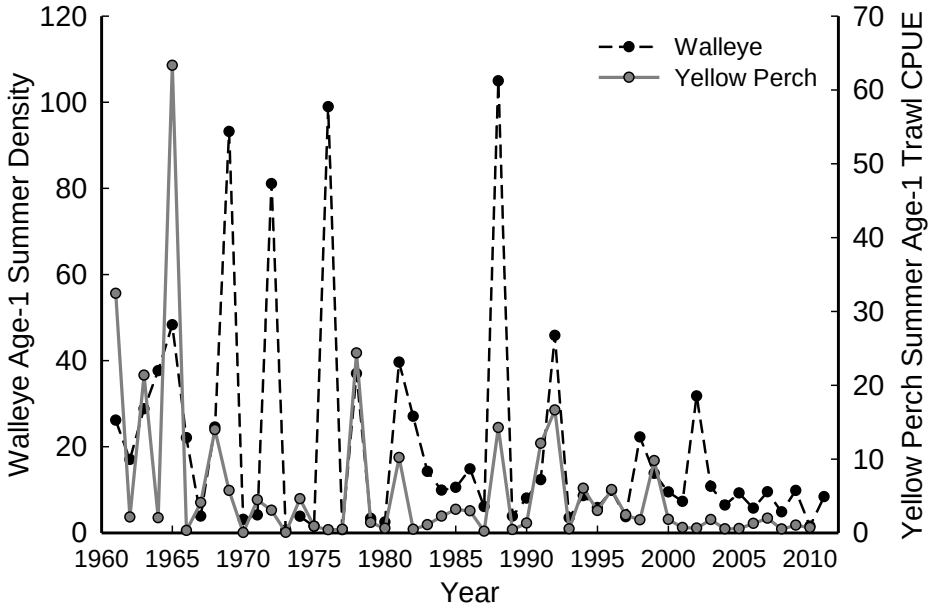


Figure 3.4. Walleye and yellow perch age-1 summer densities in Oneida Lake. Walleye densities are combined age-1 gillnet and trawl catches and yellow perch densities are age-1 trawl catch-per-unit-effort.

Table 3.4. ANCOVA results testing walleye and yellow perch year-class groupings which experienced different cormorant abundances on Oneida Lake. Year-class (YC) groupings were as follows: 1960-1988, 1989-2002, and 2003-2007/2008. Age-1 indices were used as covariates. (*) indicates equal slopes between year-class groupings.

Source	Sum of Squares	df	F-ratio	*P*	r^2
Walleye*					0.83
Ln($W_{age\text{-}1}$)	36.03	1	157.29	<0.0001	
YC	11.15	3	16.23	<0.0001	
Error	10.08	44			
Yellow Perch*					0.66
Ln($Y_{age\text{-}1}$)	26.98	1	79.01	<0.0001	
YC	24.83	3	24.24	<0.0001	
Error	15.36	45			

returned to the previous relationship (1960-1988 YC vs. 2003-2007 YC, $P = 0.64$; Table 3.5; Figure 3.5). The yellow perch ANCOVA model was overall significant ($P < 0.0001$) and both model factors were significant (Table 3.4). Differences were only found between the 1960-1988 YC and 1989-2002 YC groupings ($P = 0.0084$). Since the walleye and yellow perch adult recruitment models were not significantly different between the pre-cormorant year classes and the post-2003 year classes (Bonferroni corrected $P > 0.05$; Table 3.5), a single regression was performed for each species to establish an age-1 to adult recruitment relationship for future predictions. The resulting walleye regression predicting recruitment from age-1 to age-4 using the 1960-1988 and 2003-2007 year classes (1 SE in parentheses, n=34, $r^2_{adj} = 0.83$, $P < 0.001$) was:

$$\ln W_{age-4} = 0.730(0.058) \ln W_{age-1} - 0.037(0.159).$$

The resulting yellow perch regression predicting recruitment from age-1 to age-3 1960-1988and 2003-2008 year classes (1 SE in parentheses, n=35, $r^2_{adj} = 0.64$, $P < 0.001$) was:

$$\ln Y_{age-3} = 0.497(0.063) \ln Y_{age-1} + 1.537(0.210).$$

The proportion of missing recruits attributed to cormorant predation decreased sharply beginning with the 2002 walleye year class and the 2000 yellow perch year class (Figure 3.6), corresponding with the decreased cormorant feeding days due to cormorant hazing on Oneida Lake. The percentage of missing adult recruits averaged 29 and 47% for the 1999-2001 year classes of walleye and yellow perch, respectively, with cormorants consuming 36 and 12% of the predicted age-4 walleye and age-3 yellow perch. By contrast, the percentage of missing adult recruits averaged 30 and 0% for the 2002-2007/2008 year classes of walleye and yellow perch, respectively, with cormorants consuming only 2.1 and 2.3% of the predicted walleye and yellow perch recruits.

The best walleye adult recruitment model (most parsimonious with the data) based on

Table 3.5. Results of Bonferroni corrected multiple comparisons between walleye and yellow perch year-class groupings used in the ANCOVA analysis. Alpha = 0.05; * indicates significant difference.

Year Class Comparisons	Walleye	Yellow Perch
1960-1988 vs. 1989-2002	<0.0001*	0.0084*
1960-1988 vs. 2003-2007/2008	0.6422	1.00
1989-2002 vs. 2003-2007/2008	0.0179*	0.3220

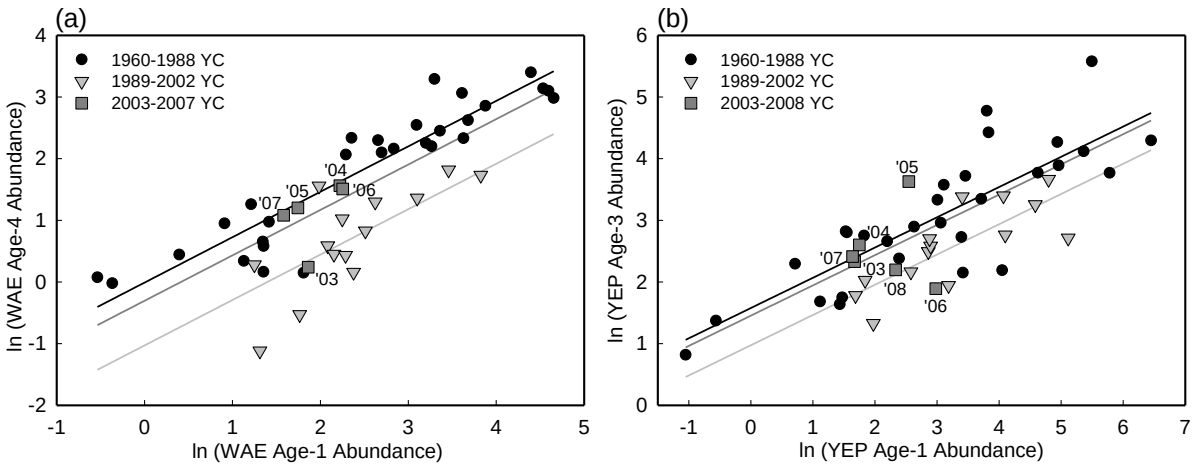


Figure 3.5. Age-1 to adult recruitment relationships for (a) walleye and (b) yellow perch in Oneida Lake for the 1960-2007/2008 year classes. Year classes were grouped according to cormorant abundance (1960-1988-low, 1989-2002-high, 2003-2007-low). ANCOVA results testing for differences between year-class groupings in found in Table 4 (equal slopes). The points for the 2003+ year classes are labeled.

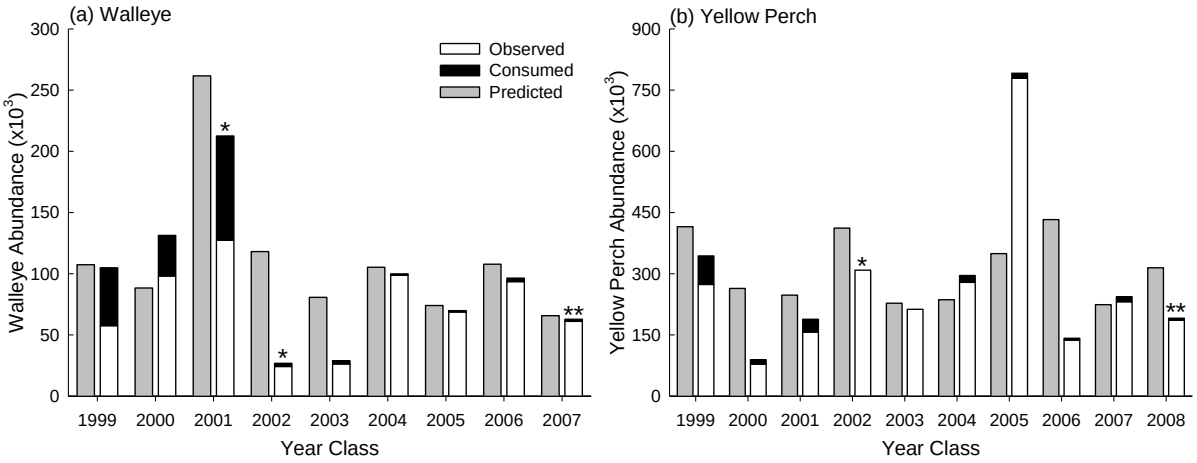


Figure 3.6. Cormorant consumption of subadult (a) walleye and (b) yellow perch compared to expected and observed age-4 (walleye) or age-3 (yellow perch) abundances in Oneida Lake for the 1999-2007/2008 year classes. Predicted age-3 yellow perch and age-4 walleye recruitment were based on the 1960-1988 year class recruitment ANCOVA models (see Figure 3.5). Information for the 1994-1998 year classes can be found in Rudstam et al. (2004). (*) indicates missing spring/summer 2004 diet information; (**) indicated missing 2010 diet information.

AIC_c analysis and model weights (w_i) for the 1960-2007 year classes included the combined age-1 index, age-2 trawl, age-2 gillnet, and cormorant feeding days (AIC_c = -71.84, w = 0.44, r^2 = 0.86; Table 3.6). The second most parsimonious model included the combined age-1 index, age-2 trawl, and cormorant feeding days (AIC_c = -71.58, w = 0.38, r^2 = 0.85). Cormorant feeding days were in the top six most parsimonious walleye recruitment models and including only cormorant feeding with the age-1 index increased the variation explained from 66% to 83% (Table 3.6). The best yellow perch adult recruitment model for the 1960-2008 year classes included age-1 trawl, age-2 trawl, age-2 gillnet, and cormorant feeding days (AIC_c = -70.16, w = 0.62, r^2 = 0.80; Table 3.6). The second most parsimonious yellow perch model included age-1 trawl, age-2 trawl, and cormorant feeding days (AIC_c = -68.64, w = 0.29, r^2 = 0.78). Cormorant feeding days were in the top four most parsimonious yellow perch recruitment models and including only cormorant feeding with the age-1 index increased the variation explained from 59 to 64% (Table 3.6).

Percid Population Simulations

Walleye: Using the historical subadult recruitment and adult survival estimates (Scenario 1) resulted in a walleye mean abundance of 708,730 (Table 3.7; Figure 3.7). If cormorant management had not occurred on Oneida Lake (Scenario 2), the adult walleye population was predicted to be at 167,870. Altering only age-4 recruitment in association with cormorant abundance (Scenario 3) resulted in a decline during the early and mid-1990s which corresponded to the observed data and then increased to a mean abundance over 235,620 adults. Scenario 4 which used the changes in age-4 recruitment and an increased adult survival from 2000-2003 simulated the observed decline and increase in abundance beginning in 2004, but then declined (diverging from observed data) and converged with Scenario 3 because both had the same adult recruitment and survival parameters. Scenario 5 simulated the decline in the 1990s and the increase in abundance during the 2000s, with an ending mean

Table 3.6. Ranked age-1 to adult recruitment models based on AIC_c and model weights (*w*) for walleye (1960-2007 year classes) and yellow perch (1960-2008 year classes) in Oneida Lake. Predictor abbreviations are as follows: TR1 = trawl age-1 (ln(catch-per-unit-effort[CPUE])) (yellow perch only); TR2 = trawl age-2 (ln(CPUE)); GN2 = gillnet age-2 (ln(catch)); COM1 = trawl age-1 (ln(CPUE)) + gillnet age-1 (ln(catch)) (walleye only); DCCO = total cormorant feeding days during ages 1 and 2 (number of days). Coefficients for predictors are located in Appendix II.

Species	Model #	Included Predictors	AIC_c	w_i	r^2
Walleye	1	COM1, TR2, GN2, DCCO	-71.84	0.44	0.86
	2	COM1, TR2, DCCO	-71.58	0.38	0.85
	3	COM1, GN2, DCCO	-69.38	0.13	0.85
	4	COM1, DCCO	-67.53	0.05	0.83
	5	TR2, GN2, DCCO	-56.86	0.00	0.80
	6	TR2, DCCO	-47.59	0.00	0.74
	7	COM1, TR2	-45.31	0.00	0.73
	8	COM1, TR2, GN2	-44.11	0.00	0.74
	9	TR2, GN2	-39.74	0.00	0.69
	10	COM1, GN2	-38.34	0.00	0.68
	11	COM1	-38.04	0.00	0.66
	12	GN2, DCCO	-35.87	0.00	0.67
	13	TR2	-35.68	0.00	0.65
	14	GN2	-18.62	0.00	0.49
Yellow Perch	1	TR1, TR2, GN2, DCCO	-70.16	0.62	0.80
	2	TR1, TR2, DCCO	-68.64	0.29	0.78
	3	TR1, GN2, DCCO	-64.48	0.04	0.76
	4	TR2, GN2, DCCO	-63.50	0.02	0.76
	5	TR1, TR2, GN2	-63.16	0.02	0.76
	6	TR1, GN2	-61.45	0.01	0.73
	7	TR2, GN2	-59.15	0.00	0.72
	8	TR2, DCCO	-58.96	0.00	0.72
	9	TR1, TR2	-57.79	0.00	0.71
	10	GN2	-51.22	0.00	0.65
	11	GN2, DCCO	-50.53	0.00	0.67
	12	TR2	-50.95	0.00	0.65
	13	TR1, DCCO	-47.58	0.00	0.64
	14	TR1	-42.46	0.00	0.59

Table 3.7. Population parameters used in simulations exploring percid population responses to changes in recruitment and adult survival beginning in 1992. Parameter estimates (years used to derive estimate in parenthesis) for each scenario and what years during simulation the estimate was used are listed. Final abundance is the equilibrium abundance.

Species	Scenario (#)	Recruitment	Survival	Final Abundance
Walleye	Historical Predictions (1)	214,000 (‘64-‘91) 1992+	0.70 (‘64-‘91) 1992+	708,730 adults
	No Management Response (2)	51,000 (‘92-‘04) 1992+	0.70 (‘64-‘91) 1992+	167,870 adults
	Change Recruitment (3)	51,000 (‘92-‘04) 1992-2004; 71,000 (‘05-‘11) 2005+	0.70 (‘64-‘91) 1992+	235,620 adults
	Short-term Harvest Change (4)	51,000 (‘92-‘04) 1992-2004; 71,000 (‘05-‘11) 2005+	0.70 (‘64-‘99) 1992-1999; 2004+ 0.93 (’00-’03) 2000-2003	235,620 adults
	Long-term Harvest Change (5)	51,000 (‘92-‘04) 1992-2004; 71,000 (‘05-‘11) 2005+	0.70 (‘64-‘99) 1992-1999 0.93 (’00-’03) 2000-2003 0.85 (’04-’11) 2004+	485,140 adults
	No Cormorant Management, Harvest Change (6)	51,000 (‘92-‘04) 1992+	0.70 (‘64-‘99) 1992-1999 0.93 (’00-’03) 2000-2003 0.85 (’04-’11) 2004-2020	345,640 adults
Yellow Perch	Historical Predictions (1)	809,000 (‘64-‘91) 1992+	0.67 (‘64-‘91) 1992+	2,492,100 adults
	No Management Response (2)	339,800 (‘92-‘04) 1992+	0.75 (‘92-‘04) 1992+	1,350,520 adults
	Change Recruitment (3)	339,800 (‘92-‘04) 1992-2004; 304,850 (‘05-‘11) 2005+	0.67 (‘64-‘91) 1992+	938,730 adults
	Change Recruitment and Survival (4)	339,800 (‘92-‘04) 1992-2004; 304,850 (‘05-‘11) 2005+	0.75 (‘92-‘04) 1992-2004; 0.71 (‘05-‘11) 2005+	1,054,980 adults

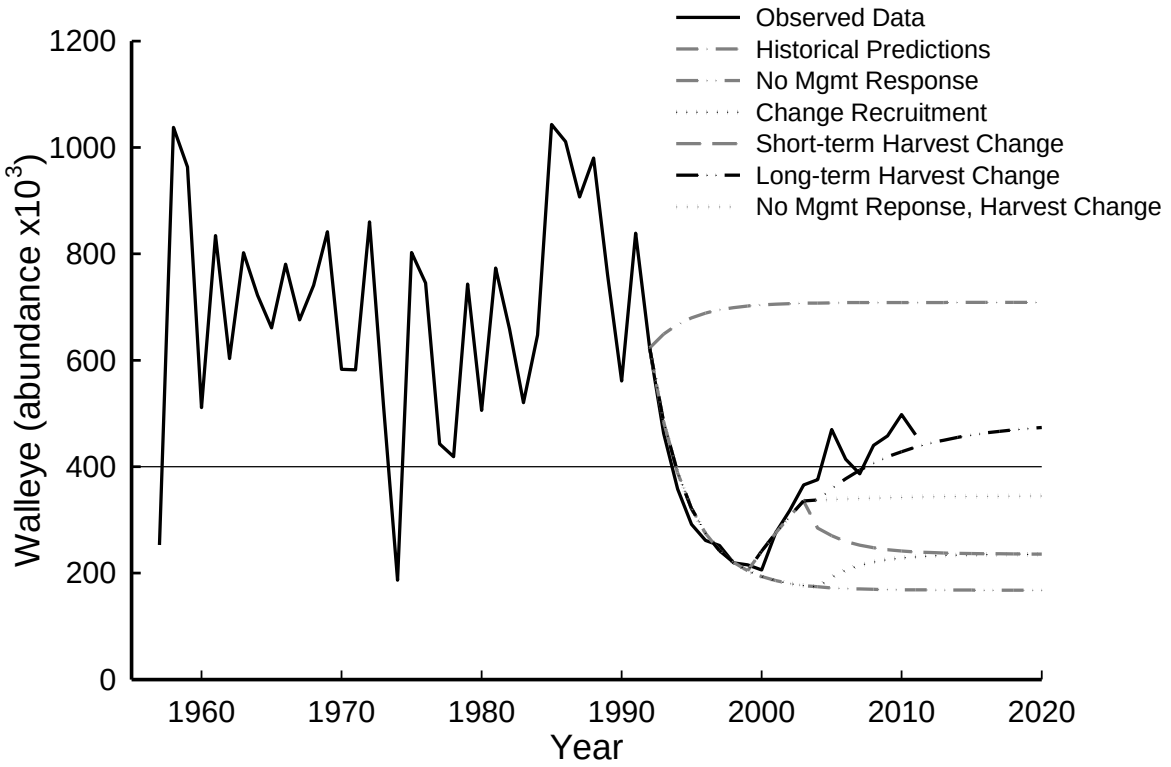


Figure 3.7. Oneida Lake adult walleye population simulations under six different age-4 recruitment and adult morality scenarios, as well as observed abundances (see Table 3.7 for scenario specifics). 'Historical Predictions' used historical age-4 recruitment and adult survival estimates. 'No Mgmt Response' used historical survival and age-4 recruitment estimates during high cormorant years to simulate population without cormorant management. 'Change Recruitment' used variable age-4 recruitment (in response to cormorant management) and historical adult survival estimates. 'Short-term Harvest Change' used variable age-4 recruitment and increased adult survival (from 2000-2003 only) from changes in walleye harvest regulation. 'Long-term Harvest Change' used variable age-4 recruitment and variable adult survival estimates in response to walleye harvest regulation changes from 2000-2003 and 2004-2011. 'No Mgmt Response, Harvest Change' used reduced age-4 recruitment and variable adult survival estimates in response to walleye harvest regulation changes. The horizontal line represents the predictions in Rudstam et al. (2004) that the walleye population would increase to 400,000 adults with cormorant management.

abundance of 485,140 adults. Scenario 6 simulated the decline observed in the 1990s and resulted in the adult population increasing prior to the observed data and an ending population of 345,640 adults. Scenario 5 was the only scenario to achieve the predicted abundance put forth by Rudstam et al. (2004) which assumed decreased age-1 recruitment (and therefore age-4 recruitment) compared to historical conditions, incorporated the lower adult numbers which occurred in the 1990s, and incorporated increased mean adult survival from 1995-2001 (0.81) compared to historical conditions.

Yellow Perch: Scenario 1 which used the historical subadult recruitment and adult survival estimates resulted in a mean yellow perch abundance of 2,492,100 (Table 3.7; Figure 3.8). In the absence of cormorant management on Oneida Lake (Scenario 2), the adult yellow perch population was predicted to be at 1,350,520. Scenario 3, varying age-3 recruitment associated with cormorant presence and using historical adult survival resulted a final abundance of 938, 730 adults. Scenario 4, using variable age-3 recruitment and increased adult survival estimates, resulted in maximum adult abundance of 1,344,460 in 2004 and after a declining population. Predictions from Scenarios 3, 4, and 5 were generally higher than observed data from 1992-2004 and closer the observed data after 2004. None of the yellow perch simulations reach the predicted abundance put forth by Rudstam et al. (2004) likely due to decreased age-3 recruitment since 2003.

DISCUSSION

Cormorant management on Oneida Lake was successful at reducing the number of cormorants on the lake and therefore the predation pressure and fish biomass removed from the ecosystem particularly from 2004 onwards. Subadult percid mortality declined after 2004 and returned to levels observed pre-1989, years with low cormorant abundance on the lake. The proportion of predicted adult recruits consumed by cormorants decreased from 36 and 12% for walleye and yellow perch for the 1999-2001 year classes to 2% for both species for

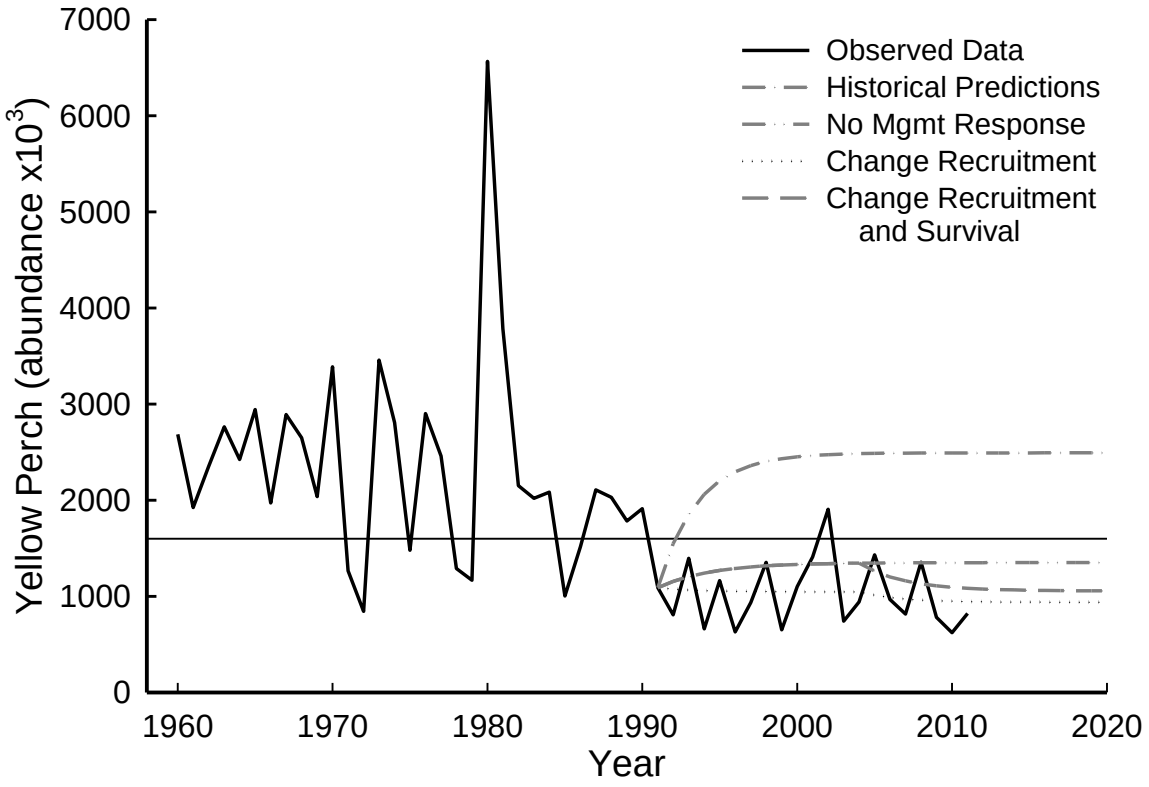


Figure 3.8. Oneida Lake adult yellow perch population simulations under four different recruitment and adult morality scenarios, as well as observed abundances (see Table 3.7 for scenario specifics). 'Historical Predictions' used historical age-3 recruitment and adult survival estimates. 'No Mgmt Response' used adult survival and age-3 recruitment estimates during high cormorant years to simulate population without cormorant management. 'Change Recruitment' used variable age-3 recruitment (in response to cormorant management) and historical adult survival estimates. 'Change Recruitment and Survival' used variable age-3 recruitment and variable (increased) adult survival estimates associated with cormorant management. The horizontal line represents the predictions in Rudstam et al. (2004) that the yellow perch population would increase to 1.6 million adults with cormorant management.

the 2002-2007/2008 year classes. Cormorant predation on percids was influential enough that cormorant abundance was included in the top 4-6 most parsimonious percid recruitment models for 1960-2007/2008 year classes. Adult walleye and yellow perch populations increased from their lowest abundances in the mid-1990s as cormorant abundances decreased. In contrast to the analysis of Rudstam et al. (2004), our manipulation was a deliberate test of the effect of cormorant predation and was not confounded by changes in water clarity caused by the invasion of zebra mussels in 1991. These results support the conclusions of Fielder (2010), Hawkes et al. (2013), and Schultz et al. (2013) who report increased fish survival and recruitment after the implementation of cormorant control. However, there were other changes in the lake during this time period, in particular an increase in gizzard shad and changes in harvest regulations that may have affected the results. We have organized the discussion into three sections: (1) evaluating the experiment testing the hypothesis postulated in Rudstam et al. (2004) that removal of cormorants would decrease subadult mortality of walleye and yellow perch; (2) comparing predictions of adult percid population levels resulting from decreased subadult mortality and the actual population development; and (3) discussing the likely effect of cormorant control on the percid populations in Oneida Lake relative to other factors.

Cormorant abundance and total consumption on Oneida Lake decreased dramatically after the initiation of cormorant management. This was expected and has been documented in other areas with non-lethal cormorant management (Dorr et al. 2012; Hawkes et al. 2013). After fall cormorant hazing began in 1998, fall consumption decreased by approximately 75%; summer consumption after 2004 decreased by over 80%. Results of the subadult mortality analyses did show a return to pre-cormorant recruitment relationships for walleye and yellow perch (Table 3.5), indicating that the reduction in cormorant predation did result in improved age-1 to age-3 recruitment, supporting the hypothesis in Rudstam et al. (2004). However, the resulting predictive equations using the 1960-1988 and 2003-2007/2008 year

classes explained less variation in age-1 to adult recruitment compared to the equations developed only using the 1960-1988 year classes in Rudstam et al. (2004) for walleye (r^2_{adj} = 0.83 vs. 0.93) and yellow perch (r^2_{adj} = 0.64 vs. 0.69), indicating more variation in age-1 to adult recruitment since 2003 compared to 1960-1988.

The subadult to adult recruitment analysis incorporating age-1 and age-2 abundance indices and cormorant feeding days as possible predictors of adult recruitment provided additional support to the hypothesis that cormorant predation had a significant impact on percid recruitment. It was not unexpected that multiple indices of cohort abundance was incorporated in the top models for both percid species; but it was interesting that cormorant abundance remained in the top six models for walleye and top four models for yellow perch (Table 3.6). The abundance measurements of the same cohort are correlated, but cormorant abundance explained part of the data variation not captured by the multiple cohort measurements; otherwise cormorants would not have ranked in so many of the top models. Incorporating cormorant predation (measured by feeding days) improved explained variation in percid age-1 to adult recruitment relationships of walleye and yellow perch by 18 and 5 percentage units, respectively (Table 3.6). This lends further evidence that the effect of cormorants on subadult mortality was significant in Oneida Lake.

Although both percid species exhibited increased adult abundance with the removal of cormorants from the system, only walleye adult abundances reached the predicted levels (400,000 adults). The walleye change point analysis resulted in multiple significant pivot years (Table 3.3), which correspond to changes in cormorant abundance and harvest regulations, supporting the recruitment analyses and the positive effects of cormorant management. Adult yellow perch abundances averaged 941,000 since the 2003 year class, compared to 1.6 million adults predicted by Rudstam et al. (2004). The change point analysis identified only a single significant shift in the yellow perch adult population over the time series (Table 3.3); providing evidence that the adult abundance has not increased since the

removal of cormorants on Oneida Lake.

The walleye population simulations revealed that the decreased subadult mortality was not sufficient to account for the observed increase in adult walleye populations (Figure 3.7). The scenarios incorporating the increased age-4 recruitment in combination with harvest regulation changes implemented in 2000 and 2004 were the most similar to the observed walleye adult population trends. For yellow perch population simulations, changes in age-3 recruitment numbers associated with cormorant abundance was sufficient for characterizing the observed data, although all scenarios predicted higher mean adult abundances during the 1990s suggesting adult survival and/or age-3 recruitment were actually lower than estimates derived from the 1992-2004 observed data (Figure 3.8; Table 3.7). Variation in year-to-year yellow perch adult survival estimates has increased since 1993 (Figure 3.9) due to limited effective mark-recapture experiments for yellow perch which were historically used to smooth adult survival estimates from the gill net; this likely affected the estimates derived for the simulations and its ability to correspond to the observed adult abundance. We did observe increased mean survival of adult yellow perch after cormorant management (compared to historical levels); however the increase in adult survival was not enough to offset the decrease in age-3 recruits every year, leading to adult populations near 1million adults. The low numbers of age-1 yellow perch occurring since 2000 (Figure 3.5) are likely reducing the number of age-3 yellow perch which are able to recruit to the adult population. However, after accounting for the low age-1 recruitment experienced in the 1999-2008 year classes, on average 13% of the predicted age-3 recruits were still missing from the population. Age-3 recruitment is still a concern for the yellow perch population, but the bottleneck has not been a result of cormorant predation on subadults since 2002 (Figure 3.6).

Even though our simulation modelling was simple, the fact that incorporating observed changes in walleye subadult recruitment did not result in a fit to the observed adult abundance requires consideration of other factors influencing adult walleye populations,

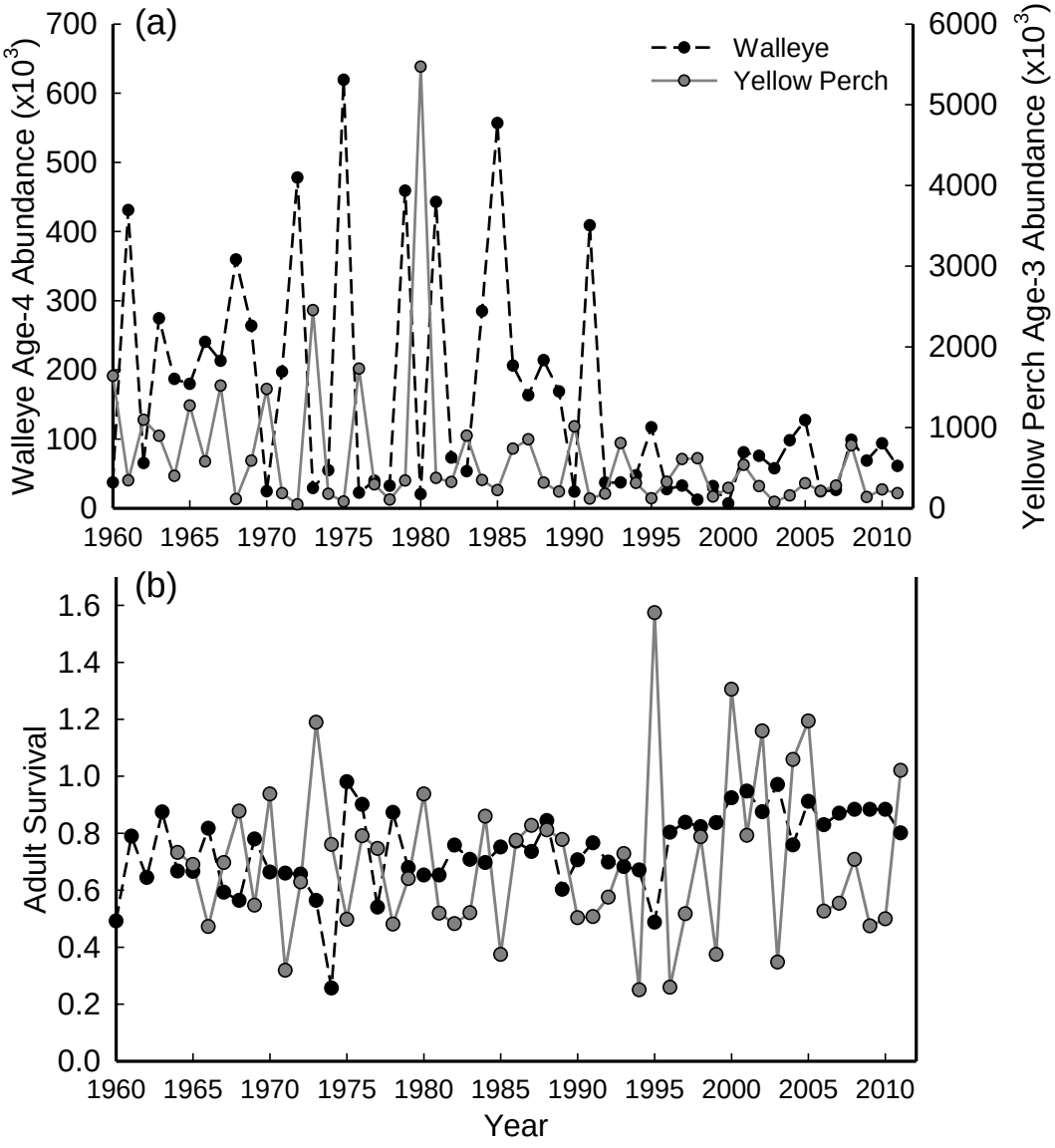


Figure 3.9. Yearly (a) age-4 walleye and age-3 yellow perch recruitment and (b) adult survival estimates (age 4+ for walleye and age 3+ for yellow perch) in Oneida Lake.

mainly adult mortality. The major source of mortality for adult walleye in Oneida Lake is the recreational fishery, which has some of the best catch rates in New York State (Krueger et al. 2009). The increase in adult walleye population levels during the early 2000s was best explained by changes in recreational harvest regulations. In 2000 harvest regulations were changed: minimum size was increased from 15" to 18" and daily bag limit was decreased from 5 to 3 fish/day. In 2004 the size limit was changed back to 15", but the daily bag limit remained at 3 fish/day. By incorporating changes in adult mortality (which decreased beginning in 1996; Figure 3.9) associated with changes in harvest regulations, the observed data were modelled accurately, indicating the angler harvest is likely the most influential factor determining walleye adult numbers.

The lack of a full recovery for yellow perch adult population could be due to many factors. Population increases only occur when the number of young yellow perch which survive to the adult stage is higher than the removal of individuals through mortality (i.e., natural mortality, predation, harvest). In Oneida Lake, production of age-1 walleye and yellow perch are at historic low levels. Yellow perch are not stocked in Oneida Lake; however walleye, a major predator of yellow perch and capable of determining yellow perch year class success in Oneida Lake (Forney 1980), are stocked at levels over 150 million fry annually (Jackson et al. 2012). By artificially enhancing the predators of young yellow perch, as well as the natural increase of other young yellow perch predators in Oneida Lake (Jackson et al. 2012; Fetzer 2013), the predatory demand on young yellow perch may be too high to permit increased recruitment to the adult population. Using a bioenergetics model, Fetzer (2013) concluded that from 2007-2009 walleye, largemouth bass and smallmouth bass (together referred to as black bass) consumed, by individual species, between 33-138 age-1 yellow perch per ha (except smallmouth bass in 2008 consumed 5.8/ha), cumulatively surpassing the estimated age-1 yellow perch density in Oneida Lake during the study. By comparison, cormorants consumed at most 71/ha in 1999 with consumption since 2000

<6.3/ha. Cormorant consumption from 2007-2009 was 0.4-1.4/ha. Fetzer (2013) determined walleye and black bass to be the primary source of age-1 yellow perch mortality during his study. The low age-1 yellow perch recruitment may be in part due to the increasing black bass population on Oneida Lake (Jackson et al. 2012) and walleye predation on age-1 during spring and summer, prior to the age-1 index being established, or the adult white perch population increasing mortality on age-0 yellow perch (Fetzer 2013).

Additionally, recruitment of age-3 yellow perch has not been at high levels for decades. From 1960-1980 there were six year classes which recruited >1 million fish, one which recruited >2 million fish, and one which recruited >5 million age-3 fish to the adult population (Figure 3.9). Yellow perch age-3 recruitment has been low since 1981, especially low since 2002 (after the removal of cormorants), with no cohort above one million recruits since 1981 except in 1990 (1.01 million fish). This 'natural' decline in age-3 recruitment coincided with the increase in cormorant presence on the lake, which in combination with the lower age-1 yellow perch abundances, exacerbated the adult recruitment problem and prevented a significant increase in the adult population.

While the increases in adult percid populations coincided with the removal of cormorants, the timing of the recovery of walleye and yellow perch should be scrutinized. A lag of 2+ years between declining cormorant predation on subadults and the subsequent increase in adult percid numbers would be expected. Since the large decline in cormorant feeding days did not occur until 2003, we would not have expected the percid populations to increase until 2005 as a response to cormorant management. However the recovery of the walleye population began in 2000, while cormorants were still at their highest levels in the study period. This may, in part, be due to the observed changes in cormorant diet composition, especially during the fall, to non-percid prey items further reducing the effect of cormorants on the sport fish populations of Oneida Lake. Cormorants select for gizzard shad and emerald shiner when available (DeBruyne et al. 2013) and it is possible that the buffering

capacity of these species allowed the percid increases prior to cormorants being removed from the system. Since the consistently large young-of-year cohorts of gizzard shad preceded the reduction in cormorant feeding days to pre-1990 levels, the benefit to the percid populations was realized earlier and the predator removal more complete (with respect to predation on percids). This is particularly true for the migrant period (fall) when gizzard shad are larger than 45 mm, the sizes selected by cormorants in Oneida Lake (DeBruyne et al. 2013). Prey selectivity by cormorants, combined with walleye harvest regulation changes, provide explanations for why the percid adult populations increased earlier than expected and emphasize that the removal of cormorants was not the only factor influencing the increase in the walleye population.

The hypothesis in Rudstam et al. (2004) that decreased cormorant numbers would reduce percid subadult mortality was supported by this whole-lake predator manipulation experiment. However, the predicted increase in adult percid abundances was not achieved for yellow perch and increased age-4 recruitment only contributed 21% of the modelled increase in the adult walleye population. Management of the Oneida Lake fishery should no longer only consider walleye and their prey species, but instead consider the suite of predators and prey species interacting in the lake. More is occurring in Oneida Lake; new processes, new interactions, new compensations of the ecosystem. New or resurging species (white perch, gizzard shad, black bass) are in the system, and contributing a larger proportion of the total biomass in the lake (Miehls et al. 2009; Jackson et al. 2012), as well as significant sources of mortality for young fish (Fetzer 2013). Reducing one source of mortality (e.g., cormorants) may be compensated for quickly by another (e.g., largemouth bass), resulting in a new food-web connection which may need to be part of management considerations.

All of these realized and potential ecological changes for Oneida Lake's future emphasize the fact that our changing climate (e.g., warming water temperatures [Jackson et al. 2008]) and new invasions (e.g., round goby discovered in Oneida Lake in 2013, Cornell

Biological Field Station, *unpublished data*) may render the previous management practice of concentrating on the walleye-yellow perch predator-prey dynamic ineffective. Cormorant foraging was a factor in the decline of the percid population and removing cormorants from the lake decreased subadult mortality and the percid adult populations stabilized in the lake; but today cormorant presence may be ecologically lessened compared to the 1990s due to their changed consumption patterns and the effects of other predators. Cormorant management was very effective at reducing cormorant foraging on Oneida Lake; however harvest regulation changes impacted the adult walleye abundance more than reduced subadult mortality. The increased predation on age-1 yellow perch from walleye and black bass populations may be currently decreasing age-1 densities and subsequently the adult yellow perch population. The percid populations may be more effectively managed using traditional fishery management methods (e.g., harvest regulation changes) compared to managing cormorants with the expectation of increased adult percid populations. The caveat of this management strategy is determining which percid species to manage for in the future: a large walleye population may suppress the yellow perch populations (Forney 1980; Fetzer 2013). Managers will need to determine the appropriate balance based on agency fishery goals and angler expectations, and the social carrying capacity of cormorant presence (Carpenter et al. 2000) and cormorant management (Kuentzel et al. 2012) on Oneida Lake. Conducting cormorant management during the entire breeding season, especially by non-lethal methods, is expensive. The level of financial commitment may not always be possible, and as such, cormorants on Oneida Lake have not been managed by USDA APHIS Wildlife Services since 2009 (DeVault et al. 2012). The system has irreversibly changed and any continued management (for cormorants or otherwise) needs to incorporate the currently available data to manage the Oneida Lake ecosystem adaptively and effectively.

ACKNOWLEDGEMENTS

Funding and support for this project was provided by New York State Department of Environmental Conservation (New York Federal Aid in Sport Fish Restoration Program); U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services; U.S. Geological Survey, New York Cooperative Fish and Wildlife Research Unit; Oneida Lake Fish Cultural Station; The Jack H. Berryman Institute; and by a grant from the U.S. Fish and Wildlife Service, Sport Fish Restoration. We thank the following individuals for their invaluable contributions to this effort: John Forney, Connie Adams, Tom Brooking, Scott Krueger, Ken Preusser, Justin Gansowski, Rich Chipman, Martin Lowney, Carl Cranker, Elizabeth Cranker, Bridger and Kelly Thompson, and the host of researchers, staff, and students who have contributed to long-term fish and waterbird monitoring efforts at the Cornell Biological Field Station. Mention of trade names or commercial products in this manuscript does not imply endorsement or recommendation for use by the U.S. Government. This is a product of the New York Cooperative Fish and Wildlife Research Unit and the Cornell Biological Field Station, Department of Natural Resources, Cornell University.

LITERATURE CITED

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458-473.

Barks, P. M., J. L. Doucette, and C. M. Somers. 2010. Lack of angling-sized yellow perch in a Canadian boreal lake: potential influences of growth rate, diet, and predation by double-crested cormorants. Transactions of the American Fisheries Society 139: 1029-1040.

Birt, V. L., T. P. Birt, D. Goulet, D. K. Carins, and W. A. Montevecchi. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40: 205-208.

Burnett, J. A. D., N. H. Ringler, B. F. Lantry, and J. H. Johnson. 2002. Double-crested cormorant predation on yellow perch in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 202–211.

Carpenter, L. H., D. J. Decker and J. F. Lipscomb. 2000. Stakeholder acceptance capacity in wildlife management. Human Dimensions of Wildlife 5: 5-19.

Claypoole, K. 1988. First nesting of the double-crested cormorant at Oneida Lake, New York. Kingbird 38: 235–236.

Coleman, J. T. H. 2009. Diving behavior, predator-prey dynamics, and management efficacy of double-crested cormorants in New York State. Doctoral dissertation. Cornell University, Ithaca, New York.

Coleman, J. T. H., C. M. Adams, M. Kandel, and M. E. Richmond. 2012. Eating the invaders: the prevalence of the invasive round goby (*Apollonia melanostomus*) in the diet of double-crested cormorants on the Niagara River. Waterbirds 35(Sp. 1): 103-113.

Connelly, N. A., and T. L. Brown. 1991. Net economic value of the freshwater recreational fisheries of New York. Transactions of the American Fisheries Society 120: 770–775.

Cowx, I. G. (Ed). 2003. Interactions between fish and birds: Implications for management. Fishing News Books, Blackwell Science, Oxford.

Custer, T. W. and C. Bunck. 1992. Feeding flights of breeding double-crested cormorants at two Wisconsin colonies. Journal of Field Ornithology 63: 203-211.

DeBruyne, R. L., T. L. DeVault, A. E. Duerr, D. E. Capen, F. E. Pogmore, J. R. Jackson, and L. G. Rudstam. 2012. Spatial and temporal comparisons of double-crested cormorant diets following the establishment of alewife in Lake Champlain, USA. Journal of Great Lakes Research 38(Supplement 1): 123–130.

DeBruyne, R. L., J. T. H. Coleman, J. R. Jackson, L. G. Rudstam, and A. J. VanDeValk. 2013. Analysis of prey selection by double-crested cormorants: a 15-year diet study in Oneida Lake, New York. Transactions of the American Fisheries Society 142: 430-446.

DeVault, T. L., R. B. Chipman, S. C. Barras, J. D. Taylor, C. P. Cranker III, E. M. Cranker, and J. F. Farquhar. 2012. Reducing impacts of doublecrested cormorants to natural resources in central New York: a review of acollaborative research, management, and monitoring program. Waterbirds 35 (Sp 1): 50-55

Diana, J. S., S. Maruca, and B. Low. 2006. Do increasing cormorant populations threaten sportfishes in the Great Lakes? a case study in Lake Huron. Journal of Great Lakes Research 32: 306–320.

Dorr, B. S., T. Aderman, and P. H. Butchko. 2010a. Management effects on breeding and foraging numbers and movements of double-crested cormorants in the Les Cheneaux Islands, Lake Huron, Michigan. Journal of Great Lakes Research 36: 224-231.

Dorr, B. S., A. Moerke, M. Bur, C. Bassett, T. Aderman, D. Traynor, R. D. Singleton, P. H. Butchko, and J. D. Taylor. 2010b. Evaluation of harassment of migrating double-crested cormorants to limit depredation on selected sport fisheries in Michigan. Journal of Great Lakes Research 36: 215-223.

Dorr, B. S., S. L. Hanisch, P. H. Butchko, and D. G. Fielder. 2012. Management of double-crested cormorants to improve sport fisheries in Michigan: three case studies. Human-

Wildlife Interactions 6: 155-168.

Farquhar, J. F., I. M. Mazzocchi, R. D. McCullough, R. B. Chipman, and T. L. DeVault. 2012. Mitigation of double-crested cormorant impacts on Lake Ontario: from planning and practice to product delivery. Waterbirds 35 (Sp1): 56-65.

Fetzer, W. W. 2013. Disentangling the effects of multiple ecosystem changes on fish population and community dynamics. Doctoral dissertation. Cornell University, Ithaca, New York.

Fielder, D. G. 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of double-crested cormorants. Journal of Great Lakes Research 34: 506–523.

Fielder, D. G. 2010. Response of yellow perch in Les Cheneaux Islands, Lake Huron to declining numbers of double-crested cormorants stemming from control activities. Journal of Great Lakes Research 36: 207-214.

Forney, J. L. 1967. Estimates of biomass and mortality rates in a walleye population. New York Fish and Game Journal 14: 176-192.

Forney, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. Journal of the Fisheries Research Board of Canada 34: 1812-1820.

Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. New York Fish and Game Journal 27: 105–141.

Fowle, M. R. 1997. Population dynamics, food habits, and bioenergetics of double-crested cormorants in Lake Champlain. M.Sc. Thesis, University of Vermont, Burlington.

Glahn, J., and K. Brugger. 1995. The impact of double-crested cormorants on the Mississippi Delta catfish industry: a bioenergetics model. Colonial Waterbirds 18: 168-175.

Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the

American Fisheries Society 117: 55–62.

Hatch, J. J. 1995. Changing populations of double-crested cormorants. Colonial Waterbirds 18 (Special Publications 1): 8-24.

Hatch, J. J., and D. V. Weseloh. 1999. Double-crested cormorant (*Phalacrocorax auritus*). *In* A. Poole and F. Gill, *eds*., The birds of North America, No. 441. Inc., Philadelphia, Pennsylvania.

Hawkes, J. P., R. Saunders, A. D. Vashon, and M. S. Cooperman. 2013. Assessing efficacy of non-lethal harassment of double-crested cormorants to improve Atlantic salmon smolt survival. Northeastern Naturalist 20: 1-18.

Hebert, C. E., J. Pasher, D. V. Weseloh, T. Dobbie, S. Dobbyn, D. Moore, V. Minelga, and J. Duffe. 2014. Nesting cormorants and temporal changes in Island habitat. The Journal of Wildlife Management 78: 307-313.

Hundt, P. J., A. M. Simons, and D. L. Pereira. 2013. Double-crested cormorants (*Phalacrocorax auritus*) of Leech Lake, Minnesota: temporal variation of diets and assessment of differential prey selection in adults. The American Midland Naturalist 169: 354-370.

Idrisi, N., E. L. Mills, L. G. Rudstam, and D. J. Stewart. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 58: 1430–1441.

Irwin, B. J., T. J. Treska, L. G. Rudstam, P. J. Sullivan, J. R. Jackson, A. J. VanDeValk, and J. L. Forney. 2008. Estimating walleye (*Sander vitreus*) density, gear catchability, and mortality using three fishery-independent data sets for Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 65: 1366–1378.

Jackson, J. R., A. J. VanDeValk, J. L. Forney, B. F. Lantry, T. E. Brooking, and L. G. Rudstam. 2008. Long-term trends in burbot abundance in Oneida Lake, New York: life at the southern edge of the range in an era of climate change. Pages 131–152 in V.

L. Paragamian and D. H. Bennett, editors. Burbot: ecology, management, and culture. American Fisheries Society, Symposium 59, Bethesda, Maryland.

Jackson, J. R., L. G. Rudstam, T. E. Brooking, S. D. Krueger, K. T. Holeck, C. Hotaling, and J. L. Forney. 2012. The Fisheries and Limnology of Oneida Lake. New York State Department of Environmental Conservation, Federal Aid in Sport Fish Restoration, Study 1,Project F-56-R, Albany.

Johnson, J. H., R. M. Ross, R. D. McCullough, and A. Mathers. 2010. Diet shift of double-crested cormorants in eastern Lake Ontario associated with the expansion of the invasive round goby. Journal of Great Lakes Research 36: 242–247.

Krueger, S. D., J. R. Jackson, A. J. VanDeValk, and L. G. Rudstam. 2009. The Oneida Lake Creel Survey, 2002-2007. New York State Department of Environmental Conservation, Albany.

Kuentzel, W. F., D. E. Capen, Z. L. Richards, and B. R. Higgins. 2012. Attitude strength and social acceptability of cormorant control programs on Lake Champlain. Journal of Great Lakes Research 38: 141-149.

Lantry, B. F., T. H. Eckert, C. P. Schneider, and J. R. Chrisman. 2002. The relationship between the abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. Journal of Great Lakes Research 28: 193–201.

Mayer, C. M., R. A. Keats, L. G. Rudstam, and E. L. Mills. 2002. Scale-dependent effects of zebra mussels on benthic invertebrates in a large eutrophic lake. Journal of the North American Benthological Society 21: 616-633.

Mayer, C. M., B. Zhu, and R. Cecala. The zebra mussel invasion of Oneida Lake: benthification of a eutrophic lake. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland. In press.

Miehls, A. L. J., D. M. Mason, K. A. Frank, A. E. Krause, S. D. Peacor, and W. W. Taylor.

2009. Invasive species impacts on ecosystem structure and function: A comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. Ecological Modelling 220: 3194-3209.

Mills, E. L., J. L. Forney, M. D. Clady, and W. R. Schaffner. 1978. Oneida Lake. Pages 367-451 in J. A. Bloomfield, editor. Lakes of New York State. Volume II. Academic Press, New York.

Mills, E. L., J. L. Forney, and K. T. Holeck. In press. Oneida Lake: a century of biotic introductions and ecosystem change. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: long-term dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland.

Neuman, J., D. L. Pearl, P. J. Ewins, R. Black, D. V. Weseloh, M. Pike, and K. Karwowski. 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54:1569–1584.

Ridgway, M. S., W. I. Dunlop, N. P. Lester, and T. A. Middel. 2012. Relative demand by double-crested cormorants and anglers for fish production from lakes on Manitoulin Island, Lake Huron. Journal of Great Lakes Research 38: 514-523.

Rudstam, L. G., and J. R. Jackson. 2012a. Yellow perch abundance and length at age in Oneida Lake, New York, 1957-2011. Knowledge Network for Biocomplexity. Available: https://knb.ecoinformatics.org/#view/cbfs.127.12. (June 2014).

Rudstam, L. G., and J. R. Jackson. 2012b. Walleye abundance and length at age in Oneida Lake, New York (1957–2011). Knowledge Network for Biocomplexity. Available: knb.ecoinformatics.org/#view/datastar.14.49. (June 2014).

Rudstam, L. G., A. J. VanDeValk, C. M. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14: 149–163.

Schneider, J. C., P. W. Laarman, and H. Gowing. 2000. Chapter 17: Length–weight relationships. Manual of fisheries survey methods II: with periodic updates. Fisheries Special Report 25. Michigan Department of Natural Resources, Ann Arbor.

Schultz, D. W., A. J. Carlson, S. Mortensen, and D. L. Pereira. 2013. Modeling population dynamics and fish consumption of a managed double-crested cormorant colony in Minnesota. North American Journal of Fisheries Management 33: 1283-1300.

Tobin, M. E., D. T. King, B. S. Dorr, S. J. Werner, and D. S. Reinhold. 2002. Effect of roost harassment on cormorant movements and roosting in the delta region of Mississippi. Waterbirds 25: 44-51.

VanDeValk, A. J., C. M. Adams, L. G. Rudstam, J. L. Forney, T. E. Brooking, M. A. Gerken, B. P. Young, and J. T. Hooper. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 131: 27–39.

VanDeValk, A. J., L. G. Rudstam, J. R. Jackson, and S. D. Krueger. In press. The Oneida Lake fishery: interactions between fishing and fish. In L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: longterm dynamics of a managed ecosystem and its fisheries. American Fisheries Society, Bethesda, Maryland.

Weseloh, D. V., C. Pekarik, R. Havelka, G. Barrett, and J. Reid. 2002. Population trends and colony locations of double-crested cormorants in the Canadian Great Lakes and immediately adjacent areas 1990-2000: a manager's guide. Journal of Great Lakes Research 28: 125-144.

Wires, L. R., F. J. Cuthbert, D. R. Trexel, and A. R. Joshi. 2001. Status of the Double-crested Cormorant (*Phalacrocorax auritus*) in North America, final report to United States Fish and Wildlife Service. University of Minnesota, St. Paul, Minnesota.

Zhu, B., D. G. Fitzgerald, C. M. Mayer, L. G. Rudstam, and E. L. Mills. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged

macrophytes. Ecosystems 9: 1017–1028.

APPENDIX II

Table AII.1. Cormorant diet composition by weight (%) for the ten species comprising largest overall diet weight from Oneida Lake from all collected samples, 1995-2009 (taken from DeBruyne et al. 2013). Percentages are from combined regurgitant and stomach samples when weight estimates were available (not available in 1997). S=summer diets, F=fall diets. No summer samples were taken in summer 2004. Sample sizes and number of identified prey are in DeBruyne et al. (2013). BUT = burbot; GIS = gizzard shad; *Lepomis* = *Lepomis* spp.; LOP = logperch; ROB = rock bass; SMB = smallmouth bass; WAE = walleye; WHP = white perch; WHS = white sucker; YEP = yellow perch.

		Species									
Year		BUT	GIS	*Lepomis*	LOP	ROB	SMB	WAE	WHP	WHS	YEP
1995	S	9.7	1.8	3.3	2.9	2.3	1.3	25.6	0.2	3.6	41.7
	F	0.4	2.6	2.3	4.2	0.0	4.7	36.5	8.5	0.0	35.5
1996	S	6.8	0.1	5.6	0.0	2.1	4.2	19.3	0.6	2.8	57.8
	F	2.0	0.0	2.6	1.6	2.6	0.8	39.0	0.2	0.2	44.8
1998	S	1.5	0.0	8.3	7.6	2.1	2.2	19.5	2.3	9.8	44.5
	F	0.0	0.0	6.7	16.1	0.0	0.0	25.2	0.0	0.0	30.2
1999	S	0.4	0.0	16.2	0.6	0.8	2.8	26.0	1.5	2.6	44.3
	F	0.0	0.0	10.9	0.0	22.1	0.0	11.4	0.0	0.0	55.6
2000	S	0.9	0.0	6.7	0.1	1.4	4.6	29.2	3.7	4.9	45.0
	F	0.0	0.0	14.9	0.1	0.0	0.0	41.9	0.0	40.1	3.0
2001	S	5.0	0.0	5.0	1.4	0.6	2.0	34.4	4.9	3.9	40.8
	F	0.0	71.5	0.1	0.2	0.0	0.3	1.6	0.2	0.0	25.6
2002	S	1.0	2.7	4.3	0.2	1.9	3.3	33.7	6.1	6.9	37.3
	F	0.0	29.0	0.0	0.0	0.0	0.0	40.2	0.0	0.0	30.5
2003	S	4.5	0.7	4.2	0.6	3.4	1.2	50.1	6.9	4.5	20.4
	F	12.3	3.8	0.0	0.0	0.0	0.0	62.8	0.0	0.0	21.1
2004	F	0.0	73.1	5.5	5.4	1.8	0.3	4.0	0.0	0.0	5.3
2005	S	62.3	0.0	0.0	0.0	0.0	0.0	35.6	0.0	0.0	0.0
	F	0.0	3.8	1.4	0.0	0.0	4.8	63.2	0.0	0.0	24.9
2006	S	17.0	50.5	0.0	0.0	13.2	0.0	0.0	0.0	0.0	19.1
	F	0.0	89.1	2.5	0.0	0.0	0.1	0.0	0.0	0.0	8.2
2007	S	13.3	0.0	0.0	0.0	8.0	0.0	0.0	22.4	0.0	56.3
	F	8.7	48.1	3.9	0.0	1.4	0.3	21.5	0.0	0.0	15.1
2008	S	5.0	22.3	5.3	0.0	3.2	0.0	23.8	26.3	0.0	8.8
	F	2.8	58.7	2.0	0.0	1.4	0.1	5.6	0.1	0.0	24.3
2009	S	0.0	12.1	13.2	0.1	9.4	0.0	6.9	14.6	0.0	43.6
	F	1.9	32.4	13.5	0.0	14.1	0.0	16.2	1.4	0.0	19.7
Overall %		3.9	9.2	5.6	1.0	2.3	2.3	27.2	3.6	3.5	38.2

Table AII.2. Ranked age-1 to adult recruitment models (with predictor coefficients) based on AIC_c and model weights (w) for walleye (1960-2007 year classes) and yellow perch (1960-2008 year classes) in Oneida Lake. Predictor abbreviations are as follows: TR1 = trawl age-1 (ln(catch-per-unit-effort[CPUE])) (yellow perch only); TR2 = trawl age-2 (ln(CPUE)); GN2 = gillnet age-2 (ln(catch)); COM1 = trawl age-1 (ln(CPUE)) + gillnet age-1 (ln(catch)) (walleye only); DCCO = total cormorant feeding days during ages 1 and 2 (number of days).

Species	Model	Intercept	COM1	TR1	TR2	GN2	DCCO	AIC_c	w_i	r^2
Walleye	1	-0.074	0.473		0.222	0.138	-4.15E-06	-71.84	0.44	0.86
	2	-0.055	0.558		0.254		-4.14E-06	-71.58	0.38	0.85
	3	-0.041	0.623			0.171	-4.54E-06	-69.38	0.13	0.85
	4	-0.011	0.761				-4.59E-06	-67.53	0.05	0.83
	5	0.185			0.489	0.298	-3.76E-06	-56.86	0.00	0.80
	6	0.362			0.708		-3.52E-06	-47.59	0.00	0.74
	7	-0.494	0.466		0.408			-45.31	0.00	0.73
	8	-0.513	0.385		0.378	0.130		-44.11	0.00	0.74
	9	-0.265			0.587	0.264		-39.74	0.00	0.69
	10	-0.529	0.643			0.190		-38.34	0.00	0.68
	11	-0.502	0.797					-38.04	0.00	0.66
	12	0.592				0.601	-4.71E-06	-35.87	0.00	0.67
	13	-0.081			0.777			-35.68	0.00	0.65
	14	0.107				0.635		-18.62	0.00	0.49
Yellow Perch	1	1.245		0.200	0.273	0.234	-2.22E-06	-70.16	0.62	0.80
	2	1.765		0.233	0.395		-2.64E-06	-68.64	0.29	0.78
	3	0.710		0.274		0.445	-1.76E-06	-64.48	0.04	0.76
	4	1.356			0.387	0.322	-2.03E-06	-63.50	0.02	0.76
	5	0.868		0.182	0.206	0.338		-63.16	0.02	0.76
	6	0.505		0.244		0.489		-61.45	0.01	0.73
	7	1.000			0.316	0.410		-59.15	0.00	0.72
	8	2.147			0.595		-2.60E-06	-58.96	0.00	0.72
	9	1.577		0.229	0.380			-57.79	0.00	0.71

Species	Model	Intercept	COM1	TR1	TR2	GN2	DCCO	AIC_c	w_i	r^2
	10	0.404				0.739		-51.22	0.00	0.65
	11	0.528				0.731	-1.13E-06	-50.53	0.00	0.67
	12	1.954			0.576			-50.95	0.00	0.65
	13	1.606		0.488			-2.44E-06	-47.58	0.00	0.64
	14	1.437		0.475				-42.46	0.00	0.59